GENERAL BOTANY FOR COLLEGES

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Instructor's Outline for General Botany

A Set of Botanical Drawings for Laboratory Use

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The Century Biological Series
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GENERAL BOTANY FOR COLLEGES

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With 252 Illustrations

267026
21. 4. 32

THE CENTURY CO.
NEW YORK LONDON

1108.

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PRINTED IN U. S. A.

PREFACE

The first edition of this textbook, published in a limited issue and devised primarily for students of a single college, has achieved such a considerable success beyond the original intention that a new and more extended treatment becomes advisable. It is singularly gratifying to find that a work which is, perhaps, something of a departure from established textbook procedure, has met with approval. Perhaps it is a sign of a change in mental climate which is going on among us.

The writer has felt for a long time the serious need for a more vivid and picturesque presentation of the subject of botany in order that the beginner might be attracted to rather than repelled by it. Furthermore, it has seemed to him that this added life might be imparted through the introduction of some of the subtler significances toward which the facts of our science undoubtedly point and which usually exercise a strong magnetic attraction upon the mind of the beginning student.

Though the time is not yet ripe for a truly synthetic science which shall concern itself with the organic whole of experience rather than with the fragment which is amenable to sensuous exploration, yet it cannot be denied that it is in this direction that the tide of advanced scientific thought is already setting. Consequently it has seemed right and proper to introduce here some of the broader speculations of my biological predecessors and contemporaries which I believe will be of particular help in pointing the college student toward the new and broader science of the future.

This book is also a challenge to the young teacher to break loose from outmoded nineteenth century conventions in biological thinking and to face forward. Upon the teachers of the coming generations will devolve an ever-increasing responsibility for straight thinking, not only within the frame of inductive science, but also in that larger universe which is often called metaphysical. If they fail in this responsibility, it is difficult to see how the world can be saved from a reactionary plunge into its ancient literalisms, with the consequent forfeit of all the knowledge which science has won with such enormous labor. I shall write further on this complex matter in the forthcoming commentary which is mentioned at the end of this preface.

This book teaches respect for facts, but only in so far as they are instruments for further accomplishment. For the fact is a window which reveals something of that significant new world within it, even as the square reveals something of the nature of the cube. It seeks to develop the intuitive perception of deeper truths; yet, at the same time, it tries to guard against premature and futile speculation — that metaphysical moonshine in which the beginner often loves to wander. It sounds the note of self-reliance and confidence, but recognizes the need for humility in the face of the "awful mystery of Existence." It is dominated by the historical note, since it would correct, so far as is intellectually possible, the delusion which time introduces into the world problem. It is deliberately written in a concise style, with the hope that it may induce young men and women to use somewhat more than 60 per cent of their mental powers, and so help to eliminate that "languor of the mind" so prevalent among college students and so inimical to their progress.

Professor Coulter once remarked that in our approach to the beginner in science we should "open the doors of the universe and turn on all the lights." The writer is heartily in accord with this sentiment. The initial steps in any science are difficult, and if the enthusiasm of the neophyte can be awakened and sufficiently sustained, the conquest is all but assured. It is hoped that the treatment of botany in this book may arouse the beginner's enduring interest.

It has been the experience of teachers who have used this book that it is well adapted to undergraduate instruction. The author has tried to keep the fact in mind that he was writing for two types of student. We have moved a long way from the select circle of young men full of professional enthusiasm who clustered about Huxley or Asa Gray. To-day college biology is often elected as part of a "science requirement." The student has no least intention of becoming a scientist, and it does not seem best to force upon him the strict discipline of a professional preparation which he will never need. This is in no sense a plea for superficiality; rather, in the face of a tendency in some quarters to weaken the standard of college instruction, we should lean slightly in the other direction. Those students who for many years have gone through the material here included will vouch for the fact that it constitutes a full-sized course. Yet I think that they have found it a living subject and one pertinent to their human interests. I would here acknowledge my gratitude to them for their sympathetic coöperation in the attempt to make botany contribute something to that intangible but very real thing which constitutes liberal culture. But while writing for the majority who have no professional interest, the author has tried never to forget the claims of the possible scientist and his need for a rock-bottom foundation of factual botany.

Part I of this book starts with the slight botanical knowledge which the student may be assumed to possess. He knows beans, though he probably never looked at one — much less, ever pondered its meaning. So, from a study of familiar seeds he is led forward to the developing seedling, and finally to the external morphology of the adult plant.

This phase of botany has lately been relegated to a minor place in collegiate instruction, not at all commensurate with its pedagogical and scientific value. The recension here presented of Gray's *Structural Botany*, reinterpreted from the modern evolutionary standpoint, has commended itself to the college student, and the method of tracing the organs through the developmental series has proved to be particularly acceptable to the undergraduate mind. In the author's own procedure, the studies upon the flower are followed by work with Gray's *Manual*.

No attempt has been made to modify the rigors of terminology. We hold that we are dealing with men and not with preparatory school boys. The roots of botanical terms have a far wider applicability than to this one science, and the college student who has been taught to look to derivations never repents the time and effort spent in mastering them.

Even as the influence of Asa Gray underlies Part I, so, after a similar fashion, Part II acknowledges its indebtedness to Professor E. C. Jeffrey. When Darwin remarked that "morphology is the soul of biology," he could only have spoken of those studies which result in the evolutionary perspective and which give significance to the facts of animal and plant structure. Modern textbook writers have been singularly slow in adopting this point of view so far as the vascular plants are concerned, and the tabulation of anatomical data after the sterile manner of the German schools is still permitted to harass the student.

Part III deals with the groups of plants. It has been difficult to keep this part of the work within reasonable bounds. The consideration of type species alone involves extended description; moreover, in our desire to give an evolutionary treatment to the fascinating story of plant life and to bring it somewhere abreast of modern knowledge, we have had to introduce considerable material not usually incorporated in an elementary textbook.

The author has made provision for the laboratory work which should accompany the study of this textbook by issuing an *Instructor's Outline for General Botany* and a *Set of Botanical Drawings for Laboratory Use*. Though the *Instructor's Outline* sets forth a system which is at variance with orthodox procedure, we believe that it will quickly recommend itself to teachers who give it a fair trial.

No system ever gives complete satisfaction. This one multiplies the number of laboratory sections, since it is scarcely to be attempted with a class of more than twenty students. It places a considerable burden upon the instructor whose ideal it is to become, for the time being, the director of a collective personality. Brains, common sense, enthusiasm, sympathy, tact, and practice in handling the Socratic method successfully are requisite to its success.

Many of the drawings in this volume are original; others are redrawn, and often more or less modified, from various authors. In all such cases pains have been taken to give credit to the original sources. From the lycopods onward a considerable number of figures in Part III are from the original plates used in the illustrations for Professor E. C. Jeffrey's *The Anatomy of Woody Plants*. For the loan of these drawings I am profoundly grateful to the author of that book, and I would also express appreciation of the courtesy of the University of Chicago Press in permitting their use.

Last of all my thanks are due to my publishers for their consent to issue a short commentary upon this textbook, wherein I have been able to develop in more detail certain wider inferences which, although not strictly a part of the science of botany, may, I hope, be a source of inspiration and help to those who would like to connect the science with the subject of human experience and with the larger background of thought which underlies all knowledge.

R. E. TORREY.

Massachusetts State College,
January, 1932

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PART I

THE STRUCTURE AND CLASSIFICATION OF SEED PLANTS

> Nous devons donc envisager l'état présent de l'univers comme l'effet de son état antérieur.
>
> — Laplace.

INTRODUCTION

Botany, the science of plants, is to be our study in the coming weeks. Were we to follow any one of a dozen conventional textbook methods, we should straightway break into the subject and start accumulating botanical facts, till at the end of the prescribed period of time, with a vast sigh of relief, we could check off one more "course" from the academic menu and, perhaps, after a brief spell of indigestion, forget all about it.

But let us suppose that we are unconventional people who really believe that a college education is a serious matter — that it means more than a certain number of passed courses, intellectual mediocrity, a country-club life, and a bachelor's degree. In that case we shall stop a few minutes at the frontiers of this world of science which we are about to enter and try to get a preliminary survey of the territory.

We are justified, I think, at the outset in asking a certain searching question which is often on the student's tongue: What good will it do me to study botany? To answer this question we may have to go outside the field of botany — outside the field of science, even — but perhaps we shall return from the excursion with a sure conviction and with some notion of the goal toward which we are proceeding.

A. THE MEANING OF SCIENCE

First of all, we need to define terms and be sure of what we are talking about. Botany is a science. Here we come to a word which we all use glibly enough, but one which very few people can really define.

If we dig to the root of it — always a good plan when we are after sharp meanings — we shall find that science comes from the Latin *scire*, "to know." Science concerns itself with knowledge, and for our present purpose we may define knowledge as the content of the mind which has been accumulated through experience. What we have experienced we know, and what has never been experienced by anybody is obviously unknown and cannot be a part of science.

Experience comes to us in several ways: through our sense organs, through our emotions, and through our reason working with the data supplied by the senses and emotions. It is probable that we all have certain instinctual and intuitional experiences to add to the other kinds. All this material, which seems to arrive in a confused jumble of impressions, is sorted and classified by the mind. After it has been organized we may call it *science*, though the term is rarely used to cover such a broad field and it may better be designated as *philosophy*.

Science, as the word is employed in everyday speech, is limited to the mass of mental matter originally derived through the senses and organized into a system by the reason. In Huxley's concise words, "Science is organized common sense." *Botany* is the organized body of all the facts about plants which men have so far been able to accumulate through the use of touch, taste, sight, smell, and hearing, along with the inferences and speculations which concern these facts.

Science, then, deals with physical things, and leaves to metaphysics all concern with conditions of existence apart from sense knowledge or outside the range of the physical senses.

B. THE SCIENTIFIC METHOD

There is, therefore, nothing very mysterious or new in the methods of the scientist. He formulates his problem, frames a scheme of logical procedure, trains his senses to report accurately, and reasons to conclusions from the data he obtains. This constitutes the *inductive method*. The great scientist is set apart from his lesser brethren by his ability to handle the final step of the procedure and to reason to definite conclusions. When Sir Isaac Newton was asked how he made his outstanding discoveries, he replied: "By intending my mind on them." When the mind is held unwaveringly and at concentrated attention upon the facts of a problem, some inner faculty of judgment and understanding becomes active and pierces to their inner meaning and significance. This power can be cultivated, and the way to it is the one suggested by Newton. If we would be something other than camp-followers of science, we must learn to concentrate, going at it with resolute will and resolved to keep up the effort in spite of apparent repeated failure.

C. THE SCIENTIFIC LAW

The explanation of the facts leads ultimately in science to the discovery and formulation of a scientific law. The word *law* as used in jurisprudence carries the sense of command or compulsion. "Thou shalt," or "Thou shalt not," says the law. But mark well that a law of Nature has no compulsion behind it. It is a statement of a process in Nature not known to vary under a given set of conditions. A certain series of events always runs in an invariable order of cause and effect — that is all we know about it. Consequently, a law of Nature implies no Lawgiver. We suspect that the invariable sequence of events which we call a natural law rests upon peculiarities of structure of the metaphysical world.

D. HYPOTHESIS AND THEORY

The words *hypothesis* and *theory* are much used in scientific writings. They are the temporary halting places to which we attain as we proceed toward the formulation of laws. An *hypothesis* is a provisional conjecture put forth to explain certain facts — somebody's guess, so to speak. It is evident that many hypotheses are bound to be short-lived: the man didn't guess right. "The track of science is strewn with the wrecks of abandoned hypotheses."

A *theory* is an hypothesis which has received a considerable measure of verification. It seems to be the right guess. If it continues to cover the facts and no exceptions can be found, it becomes a scientific law. So a scientific explanation of certain facts may start as an hypothesis and may grow up through the stage of theory till it becomes a law.

E. THE FIELD OF SCIENCE

The field which science sets out to explore, to organize, and to explain in terms of law, is tremendous — no less than the whole field of the universe which will affect the scientist's sense organs, either directly or when assisted by machinery. The constant and progressive exploration of the parts of this domain which are still unknown constitutes scientific research. Possibly never before in human history has the human race been possessed of so much detailed knowledge about the physical world as it commands to-day. Yet a great fallacy underlies the assumption that this accumulation of facts has made us wiser than the ancients. Knowledge and wisdom are not the same thing. Theoretically we might weigh and measure every grain of sand on Cape Cod and catalogue all our records in books. This would be knowledge of a sort, but what an awful weariness and how utterly futile! It is better to learn about the chemical elements and the laws of their combination into molecules and crystals. Then we can begin to get some real understanding of the grains of silica, or hornblende, or feldspar. In other words, to get a truer understanding of the sand grains we have to go behind their superficial physical properties which affect our sense organs, and study their subtler qualities.

F. SCIENCE, THE HUMANITIES, AND THE ARTS

Scientific work, as at present constituted, is concerned, then, with organizing sense data into a system of thought. It does not concern itself with human feelings. It studies the structure of an obscure worm from the sea-bottom as readily as the beauty of the butterfly's wing.

Neither has science any immediate concern with practicality. Its findings may help or they may hinder economic progress; they may mean a billion dollars' reward or death from poverty. This is not an affair of science, for science only seeks to *know*.

In opposition to this attitude, the humanities deal with the province of specifically human interests and always contain an emotional element. Such subjects are modern and classical literatures, art appreciation, and music. The humanities embody some of the subtler values which men appreciate; a sensitiveness to good literature, painting, sculpture, and music distinguishes the cultured man from the boor. For after all a man's development can be measured by his ability to appreciate a progressively subtler scale of values. Such development comes through long-continued conscientious study and contemplation, and never through the pathetic vulgarisms of "short courses," and other "get-rich-quick" schemes. There is no escalator running up Parnassus.

The problem of utilizing knowledge to practical ends is the province of the arts. "Art in general consists of the truths of science arranged in the most convenient order for practice instead of in the order which is most convenient for thought" (J. S. Mill). "Science teaches us to know — an art to do" (Jevons). It is evident that applied sciences such as engineering, horticulture, sugar chemistry, and the like are really practical arts. The fine arts are attempts to embody knowledge in such a manner and in such a form as to make an appeal to the esthetic side of man's nature.

It can be seen that the terms *sciences*, *humanities*, and *arts* refer to the trinity of man's being — to his thinking, feeling, and doing, or to his "head, heart, and hand." Each of the three may have its unpleasant side, since every virtue has its correlative vice. So the hypertrophied scientific mood, or to put it more plainly, the "swelled head," has the vice of egoism and coldness, intellectual arrogance, dogmatism, and "maniacal muck-raking for items of fact." The heaven of a scientific pedant will be a place where he can measure stones in gravel banks, plot curves of their variability, and publish abundantly.

Through the humanities, feeling may degenerate into maudlin sensibility and "emotional caterwauling"; while to be wholly practical and "vocational" is to "grub for edible roots" like some Caliban and see "no flowers upon the earth, no stars overhead."

G. SUMMARY

We have cleared the ground for the question we asked at the very outset of this introductory chapter. We know what science is; we know that it proceeds to its work by the inductive method and strives to formulate scientific laws. We have seen how science generally limits the area of its exploration to the field amenable to sensuous study; and finally we have contrasted science with the humanities and the arts, recognizing that the three are the expression of man's triune nature.

H. THE VALUE OF KNOWLEDGE

So we face our opening question again: What good will it do me to study botany? Indeed, for that matter, what good will it do me to study anything? Why not be "happy" with the conventional ditch-digger?

Well, there is a whole series of answers to this question — one for each department of the triune man. Of course this division of man into parts is rather arbitrary, for in reality there is a fusion and blending of all these elements, and this fusion makes up a man's life.

(1) *The Answer of the Hand.*

First of all, whether we like it or not, most of us have to "grub for edible roots." We must make a living if we are going to live in this world. And, indeed, without work, without an attempt to embody right thinking in right action, all study becomes a vain self-indulgence. Let us study, then, to fit ourselves for a worthy job. This is one side of the many-faceted answer to the question: Why study? It is the vocational side. Taken alone and followed to the exclusion of other phases, it leads to one of the most despicable and sordid of human types. Only when illuminated by wisdom can work become a mighty creative instrument for individual and social good. Where such wisdom is to be sought we will try to suggest later.

Let us see if college botany can justify itself when tested by the vocational motive. The human race depends wholly upon plants for its fundamental necessities of food and clothing, and without the green plant all human and animal life on the earth would speedily come to an end. Already the population of many countries is pressing so closely on the food supply that disastrous famines are of periodical occurrence. The solution of the food problem is pretty definitely botanical, for botany tells us what factors are necessary for best plant growth; it tells us where to look for new plants to supplement the dietary; it creates new and more desirable varieties; it teaches us how to prevent and how to cure the diseases to which plants and animals are subject.

In addition to feeding us, plants supply us with textile fibers; drugs derived from plants cure our diseases; plant fats and aromatic oils are the source of toilet articles; spices, sugars, and flavoring extracts enter into our confections and desserts; the alkaloid narcotic, nicotine, makes life a little more enjoyable for millions of people; woods, gums, lacquers, and dye compounds of plant origin enter into the arts in a thousand ways. Indeed, there is scarcely a worthy work in the world which is not at some point concerned with plant products. It appears, then, that botany can justify herself before the most "vocational" of tribunals.

(2) *The Answer of the Heart.*

Our second answer must be to the humanist — he who emphasizes the facet of truth which deals specifically with human problems. Botany is a subject which has always had a strong human appeal. Out of the past come strange and sometimes terrible legends of the uses of plants in ceremonial magic; the medieval alchemists seek for transforming drugs and subtle, traceless poisons. The Greeks sail the "wine-dark sea" looking for the golden apples of the Hesperides. The histories of book-printing and of inconography are closely associated with the herbal of the Renaissance. Classic and modern literatures enforce their points and ornament their pages with references to specific plants, often so precisely that some botanical knowledge at least is required to understand and appreciate them. Finally the subject of symbolism draws largely upon the plant kingdom for its illustrations. The lotus, the rose, the wheat of Ceres and the grape of Bacchus, the banyan and the ash-tree, are symbols of mighty mysteries.

There is yet another aspect of the humanistic phase of botany. Caught in the net of twentieth century industrialism, men are coming more and more to look to Nature as the best physician for weary bodies and minds. Yet to one who is untrained in Nature's ways, who is unable to hold "communion with her visible forms," who is unfamiliar with minerals, birds, insects, trees, flowers, there can be small profit in a country vacation. This is no appeal to the sentimental "nature-lover"; it is rather a recognition of the fact that names of merchants, physicians, lawyers, and clergymen have been prominent in the lists of amateur naturalists and botanists.

(3) *The Answer of the Head.*

To the critical mind with its passion for order and symmetry, botany, like all the sciences, teaches the methods of precision and intellectual honesty. Among all our pleasures none is so intensely real and permanent as the vivid sense of power and life which is the reward of intellectual work. The mind of the average student is mostly muddle and mess. He is a careless and superficial observer; his elementary concepts are hazy and inaccurate; his judgments are uncertain. This mental haze is due very largely to indolence, and it must be dissipated by rigorous discipline. And this discipline must start with voluntary attention to the solid bodies of the material world — things with sharp angles, colors, tastes, odors. Such percepts are the units out of which concepts arise. Let him observe the physical features of the earth; let him analyze minerals and rocks; let him dissect plants and animals; let him study his own marvelous body. Till he can deal effectively with these temporal and spatial things, it is futile to set him at the abstract problems of theoretical science, philosophy, and religion. Botany, then, is one of the elements which enters into that apprenticeship which the " God of Things as They Are " sets for college students in this world.

I. THE CLASSIFICATION OF THE SCIENCES

We are ready to begin our journey into the field of botany, but a prospective explorer usually wants to know the lay of the land which he intends to enter. It would be a tragedy to start for Alaska and end up in New Guinea. So let us glance at the various divisions of the scientific map and see the relation of botany to the other provinces. For just as the earth's surface is divided into geographical and political areas, so the territory of science is split up into various specific sciences. The reason is evident. It was early discovered that no one man could hope to compass the whole scientific field, and so, for convenience, it was parceled out into more workable tracts.

The fundamental divisions are largely artificial, though Nature herself seems to have suggested the two major ones, viz., the abiological and biological sciences. The former, which are not our special field at this time, may in a broad sense be divided between physics and chemistry. The latter, or biology, divides into the two sub-sciences of botany or phytology, which deals with the plant, and zoölogy, whose province is the animal. It is permissible to consider that the study of man and of his activities is also comprehended under zoölogy, but this study is usually raised to the rank of a special science of anthropology, which in its turn is divided into several sub-sciences.

J. THE SCIENCE OF BOTANY

Just as science is divided into many sciences, so botany is divided into sub-sciences, of which the following table sets forth the most important. With each term is given its etymology from the Greek or Latin.

BIOLOGY (*bios* = "life" + *logos* = "a discourse or treatise") is the science which deals with living things.

FUNDAMENTAL DIVISIONS

I. MORPHOLOGY (*morphe* = "form") is the study of forms and structures.
  A. EXTERNAL MORPHOLOGY deals with the structures which are exterior and which may be studied without dissection.
  B. INTERNAL MORPHOLOGY or ANATOMY (*ana* = "apart" + *temnein* = "to cut") is the study of structures after dissection.
    1. HISTOLOGY (*histos* = "a web") is the study of microscopic anatomy.
    2. CYTOLOGY (*kutos* = "a hollow vessel") deals with the minute structure of the cell, the ultimate morphological and physiological unit of living things.
  C. TAXONOMY (*taxis* = "arrangement" + *nomos* = "law") is the study of plants from the standpoint of their classification into groups.
  D. PALEOBOTANY (a division of PALEONTOLOGY) (*palaios* = "ancient") deals with plants of past ages which are known as fossils (*fossilis* = "dug up").
II. PHYSIOLOGY (*phusis* = "nature") is the science which deals with the functions of organisms.

DIVISIONS RESTING ON THE PRECEDING

I. ECOLOGY (*oikos* = "house") deals with the relations of organisms to one another and to their inorganic surroundings.
II. PHYTOGEOGRAPHY (*phuton* = "plant" + *gaia* = "the earth" + *graphein* = "to write") is the science which deals with the distribution of plants over the earth.
III. GENETICS (*genesis* = "creation") is the science of heredity and breeding.
IV. ECONOMIC BOTANY (*oikos* = "house" + *nomos* = "law") is the study of plants as related to human welfare.
  A. PHYTOPATHOLOGY (*phuton* = "plant" + *pathein* = "to suffer") is the study of plant diseases.
  B. PHARMACOLOGY (*pharmakon* = "medicine" or "magic") deals with plants used in medicine.
  C. BACTERIOLOGY concerns itself with one special group of plants — the bacteria. Similar sciences are ALGOLOGY, which deals with algæ; MYCOLOGY, which considers fungi; BRYOLOGY, which studies mosses.
  D. AGRONOMY (*agros* = "field" + *nomos* = "law") is the study of field crops.
  E. HORTICULTURE (*hortus* = "garden") considers plants grown on a smaller scale in the garden.
  F. FORESTRY is the management of growing timber.

We shall see later why so much scientific terminology rests on the Greek tongue. It is well to understand clearly that no new term should be allowed to slip by unlearned. The difficulties of botanical terminology are much overrated. The student should constantly have access to a good dictionary and take care to note the derivation of words. He finds that he soon acquires a set of the most commonly employed Greek and Latin roots and that most new words yield successfully to his key.

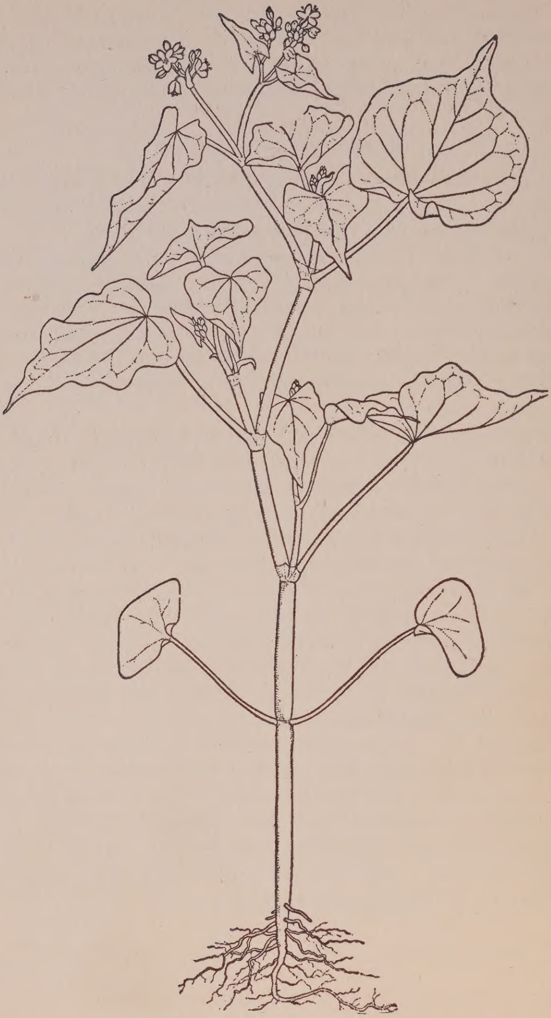
K. PLAN OF THE COURSE

With these preliminary paragraphs we have laid a foundation on which we may build our science of botany. Let us now ask ourselves at what point we may best begin our study of the plant.

There are many possibilities: we might start with the simplest known plants — the bacteria — and advance to more and more complex forms till we arrived at the flowering plants. We might begin with the morphological unit out of which plants are composed and study the way the plant body is built in its different parts. Many such different methods have been advocated; some textbooks use one method, some another.

From experience we believe that the best approach is to start with a rapid survey of a typical seed plant, then study the seed in its germination and see how such a plant actually begins its life. After this we will take up the root, the stem, the leaf, the flower, and the fruit in logical sequence. These organs will be studied in their typical forms and in some of the modifications which they have undergone to fit them for life under certain environments. To put it in more technical language: the first part of the course consists of the morphology of the spermatophytes from the evolutionary and ecological standpoints. After learning some of the facts of botany and the language of the science, we shall be in a position to identify wild flowering plants through the use of determinative keys.

Throughout the course an attempt will be made to present the successive facts as points of light which will illuminate outlying regions of the land through which we are passing. Yet in these digressions afield we shall try never to lose the main thread of the story. Rather let us consider that we are following a red thread — the story of evolving plant structures — and that the thread tints with its own color all the immediately outlying regions.



The Buckwheat Plant — a Typical Herb.

CHAPTER I

THE SEED PLANT AND ITS ORGANS

1. *Introduction*

When one enters a new region one needs a generalized map which omits all the details of rivers, hills, and forests and plays up the striking features instead. So at the outset of our botanical studies let us take a plant and learn something about its general topography. Any sort of branching weed will do nicely — ragweed, pigweed, whatever comes to hand. These herbs are all built on the same general plan, and the following description can be adapted to any of them. Lacking an actual specimen, we can make shift with the figure of the buckwheat on the opposite page.

Note first of all that the body of this typical seed plant consists of certain fundamental parts or organs. An *organ* is a part of a plant (or an animal) which has a definite work or function to perform. Thus the plant leaf-organ makes food out of water and carbon dioxide, while the animal liver secretes bile. This is obviously a physiological definition of an organ.

But an organ may also be defined as a part of a plant or animal which possesses a definite structure. This definition is particularly useful to the botanist, who finds that the plant organs can easily assume functions which are not natural to them. There are leaves, for example, which look like roots and even absorb salts and water. Physiologically they are roots, yet a study of their structure permits the botanist to pull away their disguise and to prove that they are really leaves. Hence structure rather than function reveals their true nature.

The essential organs of the seed plant are five: *root*, *stem*, *leaf*, *sporangium* or *spore-sac*, and *hair*. Every part of a plant, no matter how unlike these typical organs it may appear, may be relegated to one of these morphological categories.

Right away we see that a plant has a far lesser number of organs than has one of the higher animals. But if the plant possesses but a few organs, it has learned how to modify them very easily and to make them carry on a great diversity of functions. Just at present, however, we are not concerned with these transformations but are trying to understand the five organs in their typical unmodified conditions.

2. *The Root*

The *root* of the plant is a subterranean, whitish organ covered with lateral branches called *rootlets*. Close observation will often show that the rootlets come out one above another in vertical rows. This feature depends upon the structure of the inner parts. Were we to study the internal anatomy of a young root, we should find that the woody core bears a certain number of vertical ridges from which the rootlets arise and proceed to bore their way outward through the bark till they become free. The number of ridges, and consequently the number of vertical rows of rootlets, varies from one to ten or more, depending upon the kind of plant.

It will be noted that the main root grows vertically downward, while the lateral rootlets come out at approximate right angles and pursue an irregular path among the soil particles. They explore the surrounding soil much more effectively than we might be led to believe from observation, since in pulling a plant out of the ground one usually breaks off quantities of the more delicate rootlets.

3. *The Stem*

The *stem* can be seen to be made up of joints which owe their existence to the attachment of leaves at definite places. These points are called *nodes*, and the distance from one node to the next constitutes an *internode*. It will be further observed that a well-developed plant has a primary stem or main axis from which arise secondary branches or lateral axes. The latter will be found to spring invariably from the upper angle which the leaf makes with the stem. This is called the *leaf axil* (*axilla* = "armpit"), and so the lateral axes may be called *axillary branches*. The upper side of a leaf stalk is known as the *adaxial surface*, while its lower side is the *abaxial surface*. Consequently the upper acute angle which the leaf stalk makes with the stem is called the *adaxial angle*, while the lower and more obtuse angle beneath the leaf stalk is the *abaxial angle*.

The lateral branches, and usually the leaves of a plant, rise from the parent axis at a sharp angle. This is one of those remarkable examples of engineering which we find everywhere in Nature. The main stem, like the pillar which supports a roof, sustains the backward thrust of the side branches, heavy with their leaves and flowers. Furthermore, the leaves and branches of successive nodes are not scattered in a hit-or-miss manner up and down the stem, but their weight is distributed evenly around it. This not only enhances the architectural stability, but it avoids in large measure the shading of one branch by another.

In the upper leaf axils are found the leaf buds. They are the primordia or undeveloped conditions of the branches and are destined, of course, as time goes on, to repeat the history of the branches farther down. A well-developed lateral branch consists of a main axis and bears leaves and branches in its turn. In other words, it is a miniature copy of the whole plant.

A profound and universal law of structure underlies this fact — one which we shall come across again and again as we proceed in these studies. Throughout all Nature there is this tendency to repeat the whole in the part.

Certain minute features of the stem are usually visible to the naked eye. It may be angular due to the protrusion of woody parts which lie inside it; it may bear hairs, either individually visible or in the form of a soft plush known as *pubescence;* or it may be entirely smooth, in which case it is said to be *glabrous*. Last of all, it may be pubescent above and glabrous below, though this usually means that the hairs have fallen from the lower part. It may be reddened with a pigment (*anthocyanin*) dissolved in its sap. Sometimes the lower part near the collar is longitudinally fissured because of the expansion of the inner parts and the bursting of the outer.

4. *The Leaf*

The *leaf* is an organ which, in the typical form, consists of a flattened green blade or *lamina* of a definite shape, and a stalk or *petiole.* Two small flaps or *stipules* are sometimes found at the base of the petiole of many leaves, but in the buckwheat family, they are modified into a membranous sheath called an *ochrea*. The green color of the blade is due to a pigment known as *chlorophyll* which endows a plant, when exposed to light, with the power of making starch out of carbon dioxide and water. Through the petiole of the leaf run fibrous strands derived from the woody part of the stem; these constitute the *leaf-traces*, and through them water and salts are carried to the blade and elaborated foods are carried away from it. In the blade itself the leaf-traces break up into a network of ribs, veins, and veinlets, so that salts and water can be relayed to every least portion.

5. *The Inflorescence*

If our plant is mature enough, it may be flowering and fruiting. We should note the copious branching which brings a rather flat-topped cluster of flowers (an *inflorescence*) into existence. Each slender flower stalk is called a *pedicel;* although minute, it is a branch like any other, and it arises from the axil of a leaf. But the leaves themselves have undergone a peculiar transformation. As we trace them upward from beneath, we can see that they become progressively reduced in size and paler in color till at last they are little more than transparent, minute scales. Such modified leaves associated with an inflorescence are called *bracts*.

Here we have a first example of a plant organ transformed to something quite unlike its typical form, yet its position and the evident series of intermediate forms prove that it is really a leaf. The bracts seem to protect the soft, young flower-buds against drying out, but when the flowers have expanded, the bracts are only useless structures and are often lost. There is a striking kind of logical procedure behind this matter. Every bit of food which has come up the stem from beneath is intended for seed production, and none is available for the development of green leaves. Furthermore, they would be a useless encumbrance if they were developed, since, being so numerous, they would not only shut off light from one another but would conceal the flowers from visiting insects. Their reduction to inconspicuous bracts is a logical and satisfactory way of disposing of them.

We shall not stop now to consider the flowers and fruits. A flower is really only a collection of modified leaves borne on a very short stem and associated with sporangia. Let us rather try to pierce to the significant core of all these facts.

6. *Summary*

We cannot fail to be impressed by the neatness and precision with which the plant's body is put together in relation to the work which it has to perform. It must be carried up into the sunlight and air, and this necessitates a body which can withstand the assaults of wind and storms. So it is built with a masterly regard to the identical architectural principles which man has learned to use in the construction of buildings. Here is a slender, hollow, vertical cylinder, strengthened and buttressed on the outside, but flexible enough to give when subjected to external strains, and carrying the thrusts of lateral members symmetrically distributed around it. The lower part becomes progressively firmer as the weight above increases. Every branch is an image of the entire plant, and in its turn it becomes the parent of lesser members like itself. The lower part of the body is given over to the vegetative life; the upper part devotes itself to preparing for the next generation. With the latter function the vegetative activities are not allowed to interfere, and the green leaves are rigorously suppressed and transformed into bracts. All summer long the roots absorb water and salts while the leaves carry on an elaborate synthetic chemistry. Finally all the foods are transported upward to the precious seeds. Then the scaffolding which lifted the flowers into the air is razed and the seed falls to the earth to initiate another cycle of life. It is to the early stages of that new cycle that we turn in the next chapter.

CHAPTER II

THE SEED AND ITS GERMINATION

I. Dicotyledonous Seeds

7. The Castor-Bean (*Ricinus communis*), Spurge Family (*Euphorbiaceæ*)

The castor-bean plant has a large seed whose parts are easily visible to the naked eye. Furthermore, it possesses a type of organization which probably perpetuates the original condition of all seeds. Therefore we will select it for our introductory study of seed structure.

A warning is needed at the outset. The seeds are extremely poisonous, and two have been known to cause the death of a child who had eaten them. The strong purgative power of castor-oil is due to the small amount of poison still retained in the expressed oil. This poisonous character is shared by many euphorbiaceous plants. Several drugs are derived from the genus *Euphorbia* itself, and in preparing them the workmen suffer from headache and nausea if they breathe the vapors which rise from the vats.

The first feature which stirs our curiosity as we examine the seeds is the curious shape and coloring. It takes no great stretch of imagination to see a resemblance to a beetle. This was recognized long ago, and the name *Ricinus* means "a tick." What possible explanation can we find for such a curious fact?

There are certain evil-smelling (and presumably evil-tasting) insects which are brilliantly blotched in a similar fashion, and it is believed that birds have learned to recognize and to avoid them. The flamboyant coat is a warning sign-board. It would appear, then, that the castor-bean has come to mimic such an evil-flavored insect both in shape and in coloring; that it is mistaken for one by the birds, and is let severely alone.

Now it is one thing to recognize the advantage which the seed derives from its harlequin dress and another to explain how it originated.

A. DARWINISM

In 1859, after many years of observation and study, Charles Darwin put forward a scientific theory which attempts to explain how the present world of diversified plants and animals arose through the evolutionary process.

To begin with, it is absolutely necessary to maintain a sharp distinction between the principle of organic evolution and Darwin's attempt to give an explanation of it. Evolution is a mighty law; Darwinism is a theory.

The term *evolution* (*e* = "out" + *volvo* = "roll") simply means "a rolling out from." In other words, it is a term which refers to the development of a man, a race of organisms, an institution, an idea, a solar system, or a universe. When it pertains specifically to living things, the process is called *organic evolution.*

It is very strange that the teaching that animals and plants slowly develop through the ages could ever have excited the furious opposition of the world. No man can deny that he evolves from a speck of matter smaller than the head of a pin to an adult human being. The evolution of plants and animals from very simple beginnings to their present condition, through millions of years of geologic time, is neither more nor less wonderful. Indeed, the two processes are of an identical nature.

Have we ever stopped to wonder how a plant with all its qualities can be hidden inside a seed, or how a man can be involved in a fertilized egg? Science does not know. It sees that the part of the plant or animal which is handed on from one generation to another consists of the tiny bit of matter contributed by both parents in reproduction. This matter is called the *germ-plasm.* The portion received by each organism from its parents increases in amount in that organism's body and then is handed on by reproduction to the next generation. So the germ-plasm is immortal, though the body or soma-plasm dies with each generation. Down through the long course of the ages rolls the river of germ-plasm. But its waters undergo a continual slow change, and in consequence the bodies which it throws off successively, like water-drops, continually exhibit new features. This succession of changing bodies constitutes organic evolution.

The doctrine of organic evolution is extremely old. The Hindus and Greeks speculated about it ages ago and recognized that a chain of life had been gradually built up from the inorganic world through plant and animal and man to the divine beings or gods. Indeed, the Oriental teachings on evolution are far more searching and comprehensive than the speculations of westerners.

Charles Darwin saw that evolution was a fact and attempted to give a scientific explanation. So Darwin's explanation, which is now called *Darwinism*, or the *theory of natural selection*, is only one among many attempts to unravel the mystery. It rests upon several facts which are self-evident and need only be stated to gain our acceptance. These in essence are:

1. Over-production: Every animal and every plant produces far more offspring than can ever possibly come to maturity. Thus a single castor-bean plant may produce several hundreds of seeds in a season. Suppose all these germinate and grow to maturity and each in its turn becomes the progenitor of several hundred more offspring. In a few years the earth would be covered with castor-beans. The exact theoretical situation has been calculated for certain plants. Gager tells us that a fern plant may produce 50,000,000 spores in one season. Suppose each spore eventually produced a new fern plant and each plant was allowed one square foot of elbow-room; then the progeny of one plant for a single season would require one and two-thirds square miles of territory. Now let each of these grow to maturity and each produce 50,000,000 offspring in its turn. To accommodate them would require 83,000,000 square miles — an area nine times as great as all North America.

A mosquito hatching from the egg becomes mature and lays about 400 eggs ten days later. Half of these hatch into females. Now if a single female should hatch out on April 1, and all the progeny of succeeding generations should live, there would be on July 1, ninety days later, a total of 102,914,592,864,480,008,004,001 mosquitoes, all descended from the one original female. With such figures before us it is not difficult to realize that there is a tremendous overproduction of offspring by every plant and animal, and it is obvious that vast numbers of them can never grow up.

2. Struggle for existence: This overproduction of individuals can result in but one thing — an intense competition for the necessaries of life. Among plants the competition will be most severe among close relatives which make the same demands on the environment. Darwin called this competition the "struggle for existence." It should be realized that in this struggle success means life — failure, death.

3. Variation: No two offspring of any plant are exactly alike. Some seedlings of our castor-bean, for instance, are likely to be stronger in root and stem than their fellows. They may rob their weaker brothers of water and plant food elements, or they may grow up and overshadow and crowd them out. The superiority of a favored few leads to

4. Survival of the fittest: By "fittest" Darwin meant those organisms best adapted to the environment. If an organism should vary in a way that made it unfit for its environment, it would be promptly wiped out by its more perfectly adapted brothers.

5. The principle of heredity — like begets like: The variation which

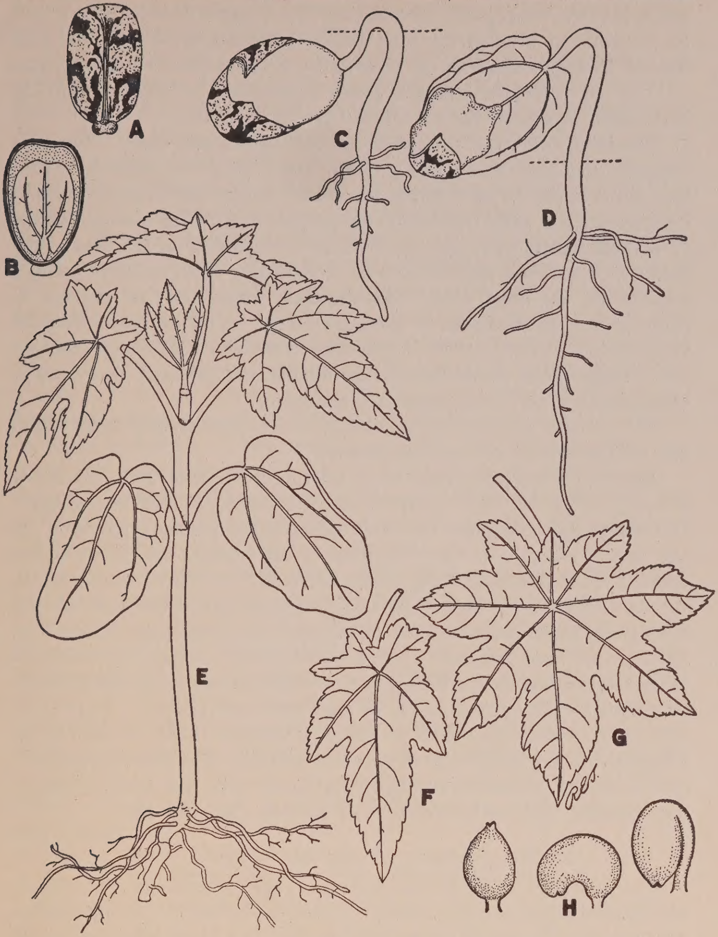


Fig. 1. — The Castor-bean: A, seed with "camouflaged" testa; B, seed in longisection showing embryo and endosperm; C, germinating seed; D, later stage in germination with endosperm nearly all absorbed; E, well-established seedling; F, first true leaf; G, later leaf type; H, the three types of ovules (orthotropous, campylotropous, and anatropous); that of the castor-bean is anatropous.

made the particular plant successful in the struggle for existence would be transmitted to offspring who would thus start life better equipped for the struggle. Such would eventually become the dominant forms.

The five principles outlined above constitute the foundation of the Darwinian theory or the theory of natural selection.

Let us apply these principles to the castor-bean seeds. We may suppose that they were originally white and that they were such conspicuous objects to seed-eating birds that many were consumed and destroyed. But they tended to vary as does everything else in Nature. If certain plants produced seeds with a slightly mottled testa, any bird which had had experience with evil-tasting ticks or beetles would pass by on the other side. The mottling would tend to increase in successive generations, since the best mimic would be most carefully avoided; so it would survive to produce descendants of similar character. Finally these would become the dominant type and a new kind of castor-bean would have come into existence.

Our work of the coming term will show us hundreds of cases which can be interpreted in a similar manner.

But is Darwin's explanation of evolution the true one? To-day it is accepted by very few biologists as a completely satisfactory theory. In the first place, it fails to account for variation among organisms. In the second place, it is very doubtful if the minute variations which Darwin made the basis of his theory are really of selective value at all. We fail to see, for example, how a slight speckling of a few seeds should have given those seeds such an advantage over their fellows that they alone would have been saved from destruction. Finally, it enthrones random chance as the governing factor which has led the world through long ages to the present state of harmony and beauty. It is more difficult to believe this than to accept a simpler theory of intelligent direction behind the scheme of cosmic evolution. But this explanation, say the critics, imports a metaphysical factor into the situation and is not scientific. So much the worse for science, then, we reply!

B. THE ANATOMY OF THE CASTOR-BEAN SEED

To come back again to the anatomy of the castor-bean seed. There are other external features besides coloring to be noted. At the smaller end is a prominent spongy outgrowth — the *caruncle* — which seems to function as an absorbent of water to facilitate germination. It may represent the remnant of an outer covering which once surrounded the seed. The nutmeg has such an outer coat, called an *aril*, which furnishes the spice known as mace, and the caruncle of the castor-bean may be a degenerate remnant of a similar organ. This suggests that structures may evolve backwards (*regressive evolution*) as well as forwards (*progressive evolution*), and pass from a state of complexity to a reduced and simplified condition.

Slightly hidden by the caruncle is a scar; it is called the *hilum* and is the point where the seed stalk was attached to the wall of the fruit. Running up from the hilum on the face of the seed is a striate band which flares a bit as it reaches the larger end and there disappears. It takes the name of the *raphe* and is really the dried seed stalk (*funicle*) grown fast to the side of the seed. In its young condition, while still in the fruit, a seed is called an *ovule*. There are three types of ovules (Fig. 1, H), and the seed of the castor-bean is derived from the most highly evolved type. If the ovule stands straight up on its funicle with its mouth (*micropyle*) at its upper end, it is said to be *orthotropous* or *atropous;* if it is bent like a curved finger so that the funicle and micropyle approximate one another due to curvature of the ovule axis, then it is called *campylotropous*. If, last of all, the ovule is completely inverted so that its micropyle lies close to the funicle attachment and points downward, then it is called *anatropous*, and this is the state in *Ricinus*. Under such a condition the funicle seems to be grown fast to one side of the ovule, and when such an ovule becomes a dry seed the withered funicle forms the raphe. The point at which the raphe flares out to join the testa is called the *chalaza;* it is really the place where the funicle joins the seed coats.

As one removes the brittle testa of the seed, a mass of white flesh or *endosperm*, surrounded by an inner friable and papery second seed coat or *tegmen*, comes into view. The endosperm is the source of castor-oil, and a bit of it rubbed on paper leaves an oily smear; the oil can also be extracted by heat and pressure or by treating the crushed seeds with a fat solvent. When the endosperm is split open, an embryo plant appears (Fig. 1, B). It consists of two evidently veiny seed leaves or *cotyledons* borne at the summit of a small, cylindric-conical *hypocotyl*. It should be noted that the latter points towards the hilum, where there is a tiny hole, the *micropyle*, not, however, easily seen in the castor-bean.

C. GERMINATION OF THE CASTOR-BEAN SEED

As soon as the seeds are placed in contact with moisture and with a considerable degree of heat, they start to germinate. First to appear outside the seed is the tip of the hypocotyl, which, elongating, pushes through the micropyle and into the earth. Meanwhile the endosperm swells from the imbibed water and splits the testa (Fig. 1, C). Nothing is to be seen of the cotyledons for several days after this, but if the endosperm be dissected away, it will be discovered that they have enlarged and have taken on a very leaf-like character, though they are still pale in color. It may also be observed that the inner surface of the endosperm where it contacts the cotyledons is wet and slimy. Actually the cotyledons have secreted a fat-splitting enzyme — lipase — which is digesting the oil of the endosperm and making it fit for osmotic absorption. On this food, provided by the mother plant, the embryo feeds while it is developing its root system and preparing itself for an independent life.

As the days pass, a strong, branching root develops from the tip of the hypocotyl, and the cotyledons, with the last remnants of the endosperm clinging to them, pull out of the soil (Fig. 1, D). The method of withdrawal is ingeniously designed to prevent any tearing of the delicate parts, for at the top of the hypocotyl a strong arch develops and heaves up the earth; then as the arch straightens out the seed leaves are drawn into the air without injury. Most seedlings develop this arch as they leave the soil.

By this time the cotyledons are well developed; their blades are oval in shape, borne on petioles, and of a vivid green color. At the junction of blade and petiole are usually to be seen small yellowish swellings, called *extra-floral nectaries*, which secrete a sugary fluid. They are also found on the adult leaves and may be of value in attracting pollinating insects to the plant.

Between the cotyledons a leaf bud has also begun to grow; in many seeds it is well developed before germination, and it then takes the name of the *plumule*. As the days pass, the plant assumes the appearance of Fig. 1, E. Its first two leaves are usually obscurely trilobate, with the middle one of the three lobes much elongate; furthermore the petiole is attached near the margin (Fig. 1, F). The later leaves increase the number of lobes and assume an orbicular form, while the petiolar attachment approaches nearer to the center. A leaf taken from an old plant is orbicular in outline with many pointed, serrate lobes, and the petiole is nearly centric in attachment (Fig. 1, G).

D. THE THEORY OF RECAPITULATION

The life history or evolutionary history of any plant or animal which begins with the fertilized egg and ends with death, constitutes the *ontogeny* (*ontos* = "being" + *genesis* = "creation"). But the individual belongs also to a long line of organisms which has been reproducing itself on the earth for millions of years. So the organism has a racial history which runs back into the remote past. This constitutes the organism's *phylogeny*. It is believed by many biologists that "ontogeny recapitulates phylogeny."

To make this formidable expression clear, let us glance again at the successive leaves developed by the castor-bean plant. The first is long and pointed, the second almost orbicular and many-lobed. Now suppose we should find a fossilized mature leaf of an ancestor of the castor-bean that lived in the Cretaceous Period. I wager that it would resemble the long, pointed, first true leaf of our modern seedling. The round, much-lobed type of leaf characteristic of the mature plant of to-day had not yet arisen in the phylogeny of the castor-bean group. This theory must not be carried too far; perfect recapitulation is exceedingly rare, and it is often obscured by adaptations and *acceleration*. The latter term means that the more remote a structure is in geological time, the more the modern growing plant tends to hasten over it, or even to drop it out of the ontogeny altogether. We believe, for example, that the extremely remote ancestors of the castor-bean were ferns, and yet no seedling castor-bean ever produces a fern leaf in its ontogeny. The doctrine of recapitulation is sometimes called the *biogenetic law*. It has rendered immense service to biology in giving us hints concerning the phylogeny of certain groups. Some of these hints have been confirmed by the discovery of fossils. For instance, no adult living bird has teeth, yet embryo chicks develop dental ridges which are absorbed before the chick hatches; several Jurassic and Cretaceous fossil birds are known which possess a whole battery of sharp teeth like the reptiles from which they evolved.

8. The Garden Bean (*Phaseolus vulgaris*), Legume Family (*Leguminosæ*)

A. ANATOMY OF THE SEED

The garden bean belongs to a more highly evolved family than does the castor-bean; its seed is derived from the type of ovule called *campylotropous* (Fig. 2, A). The hilum is a white scar on one face and at one end of the hilum lies a small heart-shaped *caruncle*. The micropyle, not easily seen in the castor-bean, is here a tiny, though conspicuous, hole leading into the seed. To understand how the micropyle comes into being, imagine the cup of an acorn to grow upward until it should almost cover the acorn itself except for a small hole at the top. In a very similar way the micropyle arises through the overgrowth of the inner part of the ovule (*nucellus*) by the outer coverings (*integuments*). To make the analogy between acorn and bean closer, one must imagine a subsequent curvature of the axis of the acorn so that it comes to resemble a crooked finger. Physiologically the micropyle serves to admit the pollen tube during the process of fertilization, and in the mature seed it serves as a point of entrance for water and a point of egress for the hypocotyl.

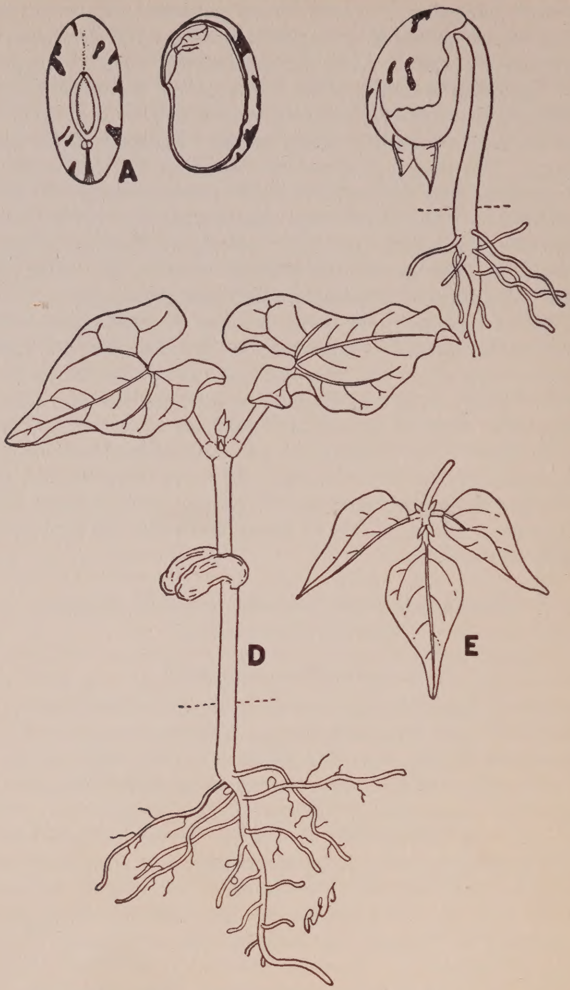


FIG. 2. — The Garden Bean and Its Germination: A, seed in face view; B, seed split open showing cotyledon, hypocotyl, and plumule; C, germinating seed; D, well-established seedling with withering cotyledons and first true leaves; E, second leaf for comparison with first.

When the testa of the bean is removed, it is seen at once that, unlike the castor-bean, the inner part is not a single mass but consists instead of two thick lobes — the halves of the bean — which are attached to a small cylindrical pointed structure. The latter fits into a shallow cavity in the testa and points toward the micropyle. Upon separating the halves of the bean, a tiny stem bearing a leaf bud is seen between them (Fig. 2, B). By comparison with the castor-bean we decide that the lobes of the bean must be the cotyledons and that the pointed cylinder is the hypocotyl. The cotyledons are bent sharply downwards, but as germination commences they rise like opening wings and stand out at right angles from the hypocotyl. The structure between them is a particularly strongly developed plumule made up of a small stem segment (*epicotyl*) and a leaf bud.

Now comes the crucial question: Where is the endosperm? Obviously it is not present, but may there not be a significant correlation between its absence and the swollen form of the cotyledons?

When a garden bean is in process of formation in the pod, it has plenty of endosperm (recall the biogenetic law), but as the cotyledons mature they absorb it into themselves, thus becoming gorged with food and much swollen. In other words, the garden bean does not wait till the time of germination to digest and absorb its food as the castor-bean does, but instead takes it completely into its cotyledons while the seed is maturing. Thus the garden bean has shunted back into its embryology a process which the castor-bean defers until the time of germination.

A seed of the type of the castor-bean is called *endospermous;* one like the garden bean is *exendospermous*. Exendospermy is biologically superior to endospermy, since it shortens the critical period of germination; no longer is it necessary for the embryo to waste time digesting and absorbing endosperm.

As the garden bean develops, the cotyledons undergo a significant modification; they are drawn up into the air and there turn green, just as they do in the castor-bean (Fig. 2, C), but as they give up their food to the developing plant they become shrunken and yellow and after a few days drop off (Fig. 2, D).

This introduces us to a whole set of fundamental biological principles.

B. COMPARATIVE MORPHOLOGY AND ITS METHODS

Over and over again in our studies in biology we shall see that plant and animal organs are extremely plastic and that their variations and adaptations lead them to assume many shapes. We have learned already that a flowering plant consists of five fundamental mosphological parts: root, stem, leaf, sporangium, and hair. As they are molded by evolution, these parts may come to mimic one another very closely.

One of the divisions of biology is comparative morphology — a study which attempts to trace out homologous organs under their various disguises. Huxley puts it thus in his inimitable way:

> "Take a science of which I may speak with more confidence and which is the most attractive of those I am concerned with. It is what we call morphology, which consists in tracing out the unity in variety of the infinitely diversified structures of animals and plants. I cannot give you any example of a thorough æsthetic pleasure more intensely real than a pleasure of this kind — the pleasure which arises in one's mind when a whole mass of different structures run into one harmony as the expression of a central law."

As an example of the methods of comparative morphology, let us ask the question: To what morphological category do the cotyledons of the garden bean belong?

1. They are borne in the same relation to the hypocotyl as are the obviously leaf-like bodies of the castor-bean, and from between them rises the plumule as in that plant.
2. They turn green upon reaching the air, and this is another normal leaf feature.
3. Minute buds occur in their axils, and if the plumule be destroyed, they will grow out into branches. But buds arise in the axils of *leaves*.

From these considerations we are justified in affirming that the cotyledon of the garden bean is a leaf so modified by evolution to fit it for the storage function that it has almost lost its leaf characters.

C. THE LAW OF IRREVERSIBILITY

An interesting question may now be raised. Could the garden bean ever turn round on the pathway of evolution, unspecialize its cotyledons and restore them to the thin leaf form again? This question (allowing for a certain amount of temporary and usually teratological atavism) must probably be answered in the negative. There is a principle known as the law of the irreversibility of evolution, which declares that organs which become too highly specialized never return to the generalized condition again, and organs which are lost entirely (such as the legs of snakes) can never be restored in later ages even if a demand arises for them again. Intense specialization is therefore dangerous for organisms which may land in a *cul-de-sac* of morphology from which there is no escape.

Returning to the bean plant, we may observe another excellent illustration of the law of recapitulation in the successive leaf shapes of the seedling. The first leaf has a simple deltoid or oval blade; the second is palmately trifoliolate (Fig. 2, D, E).

9. The Garden Pea (*Pisum sativum*), Legume Family (*Leguminosæ*)

The ordinary garden pea belongs to the same family as the bean, but it exhibits a significant difference in its method of germination. From an examination of the soaked seed the nature of the parts is plainly evident, since they correspond point for point with those of the bean. The cotyledons, however, are decidedly more bulky than in the bean — in fact they are practically hemispherical. Thus the pea has the maximum storage volume for its size which is possible to a seed.

Now if we observe the germination of the pea seed, we shall see that the cotyledons do not come above the soil. The plumule of the bean reaches the air through the elongation of the hypocotyl, but in the case of the pea the hypocotyl does not elongate; instead it is the lengthening of the epicotyl that brings the plumule out of the ground (Fig. 3). This method of germination in which the cotyledons remain beneath the soil is called *hypogean*, in contradistinction to *epigean* germination in which they rise into the air due to hypocotylar elongation.

How is hypogean germination to be interpreted? Obviously the cotyledons are hemispheres; they have departed so far from the ancient leaf condition that they can no longer serve as leaves at all but have adapted themselves wholly to the storage function and remain under ground where they are safe from desiccation. Thus the pea has advanced one stage beyond the bean and has reached the logical conclusion of this special line of evolutionary modification. As to the morphology of the cotyle-

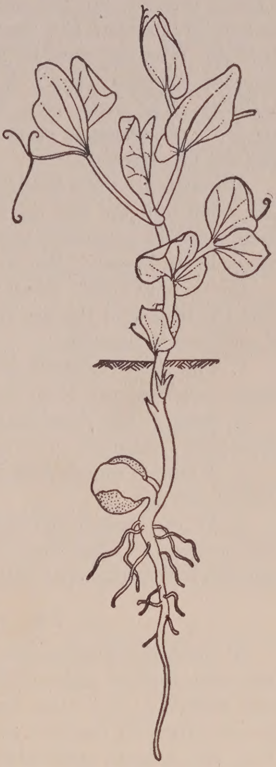


FIG. 3. — The Pea Seedling. The bulky cotyledons remain beneath the soil (hypogean germination).

dons, the same reasoning applies as in the case of the bean; they are swollen storage leaves.

10. *Phylogenetic Inferences*

To guard against a misconception which might arise in the student's mind, it should be pointed out that we do not assert that the garden bean arose from the castor-bean and the pea from the garden bean. This certainly is not the case. We have but taken these three seeds as type illustrations of a process which has worked out in many plant families. The pea and the bean are closely related plants, and their common ancestor cannot lie very far back along the phylogenetic highway. The castor-bean on the contrary must have departed ages ago from the ancestral stock which was common to the *Euphorbiaceæ* and the *Leguminosæ.*

The metaphor of a branching tree is much used by the evolutionist. The bean and the pea represent two terminal twigs of such a tree; their union in a common leguminosan branch is not far distant. The castor-bean, however, lies on another branch entirely.

Let us now briefly recapitulate the evidence which seems to prove that the bean and the pea evolved from an ancestral stock possessed of endospermous seeds:

1. The most primitive families of seed plants have endospermous seeds. Endospermy is an archaic seed feature.
2. Some living *Leguminosæ* have seeds with a small amount of endosperm; these are to be looked upon as persistent primitive types.
3. A graded morphological series can be traced from such seeds to that of the pea.
4. All pea seeds in the early stages of their embryology have abundant endosperm, and since ontogeny recapitulates phylogeny we are justified in inferring that the ancestral seed was endospermous.

11. *The Theory of Orthogenesis*

At this point it seems desirable to bring forward a theory which has been advanced to account for such a seriation of organs as we have been studying. It is clear that a line of evolution can be traced from certain primitive legumes with endospermous seeds, leaf-like cotyledons, and epigean germination through the bean, which has but recently acquired exendospermy, and has not yet wholly lost the leaf function of its cotyledons, to the pea, which is exendospermous and hypogean in germination, and whose cotyledons have become efficient storage organs with a correlated loss of the leaf function.

Such a series is called *orthogenetic* by some biologists. The word itself carries the idea of "straight evolution" and implies that when organisms (or organs) start to vary along certain lines, they continue varying along these lines independently of the action of natural selection or of other external factors. It suggests that in the organism's own make-up there is some unknown principle leading to this modification in a straight line. Orthogenetic development sometimes leads to extreme results, and bizarre forms may be brought into existence which are so ill adapted to their life conditions that natural selection is bound to wipe them out. The evolution of the horse's hoof is often cited as a case of orthogenesis. The horse was originally a small animal with five-toed feet. Geologists have discovered all gradations from this "primitive pentadactyl ungulate" through various three-toed horses to the modern *Equus caballus* which walks on the thick nail of his greatly enlarged middle toe. Even our living horse has small bone remnants of the ancestral other toes, and colts have been born with two small lateral hoofed toes much like those of their ancient forbears which once roamed over the American continent. Here, then, is an orthogenetic evolution for which Darwin's theory does not seem to be an explanation. We shall find many other cases among plants as our work advances which seem to be susceptible to the same explanation. The great difference between the Darwinian theory and the theory of orthogenesis is that the latter denies the all-sufficiency of natural selection to evolve new forms from small fortuitous variations.

There are some very profound problems connected with these matters. As long ago as 1866 Alpheus Hyatt * made a careful study of the fossil cephalopod molluscs and came to the conclusion that there is unmistakable evidence that the shells of some of these creatures went through stages of progressive coiling, till, arrived at a condition similar to that of the living pearly nautilus, they proceeded to uncoil and to return to the state of a straight shell. This progressive and regressive phylogeny required untold millions of years of Paleozoic and Mesozoic time to run its full course.

More than that, it was demonstrated that the individual creature recapitulates the racial history, and that a member of one of the senile races starts its life with a small, tightly coiled shell, which straightens out as the ontogeny progresses. In Hyatt's own words: "The young have been repeatedly shown to be close coiled and they grade into the normal progressive (straight) shells by all of their adult characters."

Finally it was proved that the senile stages of the individual of an earlier type anticipate and are parallel to changes which later overtake the race. This seems to correspond to the theory that old men foreshadow the state which the human race may one day attain as a whole.

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* A. Hyatt, "On the Parallelism between Stages in the Individual and Those in the Groups of *Tetrabranchiata*," *Mem. Bost. Soc. Nat. Hist.* (1866).

The whole subject is a complex one but it is too important to leave without a slight attempt at interpretation. Consider our own life history. We arise from the prenatal darkness, ascend through stages of childhood to the meridian of adult life, and then decline into senility till death "closing your account and mine" conducts us to the "underworld." The story visualizes itself as a curve of growth with ascending and descending limbs, and the descending stages of our "second childhood" are curiously like those of the ascending childhood. And this is exactly what Hyatt discovered about the race of coiled cephalopods, though its life, instead of covering a brief three-score and ten years, extended over millions of years.

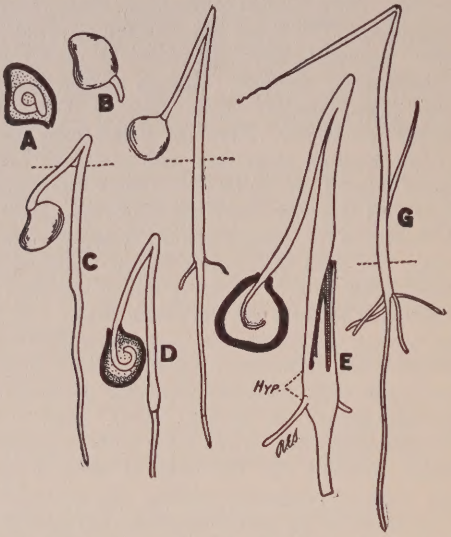

FIG. 4 — The Onion Seed and Its Germination: A, seed in longisection to show coiled embryo imbedded in endosperm; B, egress of primary root-tip and hypocotyl; C, cotyledonary arch appearing above soil; D, same stage as C to show absorbing tip of cotyledon still imbedded in endosperm; E, a stage slightly later than C with whole seedling in longisection to show extent of hypocotyl and the plumule encased in its sheath; G, later stage with plumular leaf pushing from its sheath.

II. Monocotyledonous Seeds

12. The Onion (*Allium Cepa*), Lily Family (*Liliaceæ*)

Thus far we have been studying seedlings possessed of two cotyledons. In technical terms they are said to belong to the class *Dicotyle-*

doneæ. There is, however, another class of flowering plants whose seedlings have but one cotyledon, and it will be worth while to study a representative series of them.

One of the most primitive types of monocotyledonous seeds is that of the onion. When it is sliced open parallel to its flat face, one sees a mass of whitish endosperm and imbedded in it a tiny, yellowish, thread-like embryo, bent almost into a circle and seemingly wholly undifferentiated (Fig. 4, A). It really consists of one cotyledon and a short, knot-like hypocotyle. As the seed germinates, the hypocotyl pushes through the micropyle and enters the soil, developing a root there and drawing out the thread-like cotyledon after it (Fig. 4, B, C). The tip of the cotyledon remains in the seed absorbing endosperm (Fig. 4, D), but its main body develops a strong arch and breaks through the soil. Sometimes the tension of the arch becomes so great that the seed is jerked out of the earth completely. To all appearances the embryo plant is still a single green leaf, but razor sections show that at the top of the knot-like hypocotyl (Fig. 4, E, Hyp.) a plumular leaf is beginning to develop. At first it is concealed in a tiny pouch or invagination which lies in the base of the cotyledon (Fig. 4, E), but it soon begins to grow, and pushing out of its pouch appears above the soil (Fig. 4, G). Little does this seedling resemble any that we have seen before, but careful study assures us that it is strictly comparable. The chief difficulty of interpretation lies in realizing that the green thread is really a cotyledon and that the hypocotyl is a mere knot.

From many lines of evidence botanists to-day believe that the monocotyledons had a dicotyledonous ancestry, and they see two possible ways in which the single cotyledon may have been evolved from the double.

1. The two cotyledons of the ancestral dicotyledonous seedling may have fused to form one, or

2. One of the cotyledons of the ancestral form may have gradually degenerated till finally it was gone entirely and a monocotyledonous condition resulted.

Both these views have been advanced, and there is morphological evidence for both of them which leads some botanists to believe that the monocotyledons are not monophyletic but are diphyletic or even polyphyletic. It is of some interest to formulate a mental picture of a seedling of a hypothetical dicotyledonous ancestor of the onion. Such hypothetical creations are often helpful to our understanding, but it must be clearly understood that a man enthusiastic to establish a theory may come to believe in such an "ancestor" which never had any existence outside his own head.

13. The Seed of the Date-Palm (*Phœnix dactylifera*), Palm Family (*Palmaceæ*)

The seedling of the ordinary commercial date may now be studied and compared with that of the onion (Fig. 5). Germination begins in exactly the same way; the hypocotyl emerges from the "stone" and enters the soil, developing a primary root there which is remarkably long and is probably adapted to the dry desert soils where the date-palm commonly lives and where the water table lies deep. The cotyledon, too, comes out of the seed, just as in the onion, but it never develops an arch or breaks through the soil, and since it remains underground no chlorophyll develops in it. Its sole function seems to be to digest and absorb the endosperm and to transmit it to the growing leaves and roots. First to appear outside the cotyledonary tube is the first leaf; it is only a yellowish sheath, and sometimes it does not break through the earth. The first chlorophyll-bearing organ is the second leaf — a long lanceolate or linear strongly-plaited blade. The so-called "character-leaves" of palm seedlings with their pinnate or palmate

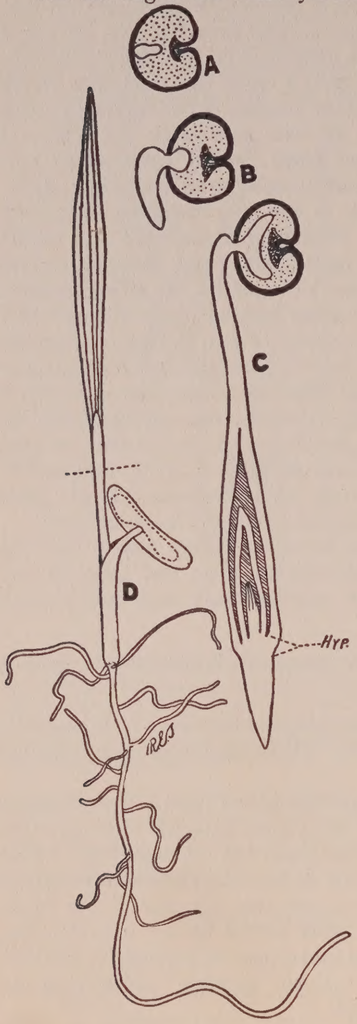

Fig. 5. — The Date and Its Germination: A, date-stone in cross-section, showing small embryo surrounded by endosperm; B, germination stage with protruding root and hypocotyl; C, longisection of seedling showing cotyledon with its pouch containing two plumular leaves; also the abbreviated hypocotyl, Hyp. and the peg-like root; D, established seedling.

blades are long delayed; once again we witness an example of the law of recapitulation.

A little thought shows us that the only significant difference between the seedling of the onion and that of the date is this: the cotyledon in the latter has lost its leaf function and remains below the surface somewhat as in the pea. But at this point the resemblance to the pea ceases, for whereas the pea cotyledon gave up its leaf function in order to become a more efficient storage organ, the date cotyledon seems to have been modified from its ancient leaf nature into an organ to digest endosperm and transmit it to the seedling. So in the *Palmaceæ* even as in the *Leguminosæ*, the cotyledon has been specialized for a new purpose and has lost its original leaf function.

14. The Indian Corn (*Zea Mays*), Grass Family (*Gramineæ*)

It is in the corn grain that this principle of specialization and reduction, initiated in the date, reaches its logical limit.

The corn grain (Fig. 6, A) consists of a mass of endosperm enclosed in protective coats. It is differentiated into a yellow, hard or corneous endosperm, and a white, softer and more loosely organized part termed *floury* or *fari-*

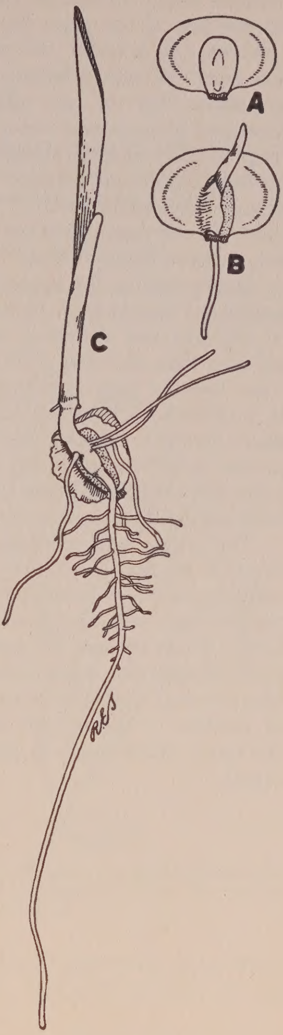

Fig. 6. — The Corn Grain and Its Germination: A, the grain with outline of plumule and root on the face of the shield-shaped cotyledon, which in its turn is surrounded by endosperm; B, plumule and root bursting through pericarp; C, established seedling — the cotyledon is stippled; adventitious roots arise from the base of the epicotyl and from the first leaf node.

naceous endosperm, though there is no real difference between them. The apparent difference is due to the fact that the floury portion contains many air spaces and its starch is more loosely arranged. On one side of the grain lies a shield-shaped body often called the *scutellum*. It is really the cotyledon, but so remarkably modified that even the trained botanist has difficulty in interpreting its various parts. On its face and slightly embedded in it lie a well-developed plumule and a root or *radicle*. The hypocotyl and epicotyl are practically lacking, though in the young seedling a well-developed epicotylar internode appears. It is said that in the plumular bud are wrapped the primordia of all the leaves and internodes which the corn plant will ever bear; thus the embryo is more strongly developed than any we have studied before.

In germination the cotyledon never leaves the grain (Fig. 6, B, C); it does not even increase in size, but is given over entirely to the work of softening and absorbing the endosperm. Nothing could look less leaf-like than this odd shield-shaped body, but our studies on the onion and the date show how it probably came to its present form. It is difficult to think of the cotyledon evolving any further in the same direction. Just as the pea cotyledon has reached the limit of storage specialization of the dicotyledonous series, so the corn cotyledon has reached the limit as a specialized digestive and absorptive body among the monocotyledons.

The young corn seedling shows several interesting features. It develops no hypocotyl, but above the cotyledon a cylindrical axis carries up the first sheathing leaf and may be called an epicotyl. At the first node and often from higher ones, too, adventitious roots put forth. These become the strong prop or brace roots of an old corn-plant, though they are also engaged in taking in water and food salts. The corn leaf consists of a sheath and a strong parallel-veined blade; at junction of sheath and blade is a membranous upgrowth called the *ligule* which seems to prevent rain-water from running into the sheath.

CHAPTER III

THE ROOT

We have seen the seedling thoroughly established in the soil. Our next studies will be concerned with the adult members of the plant and the various evolutionary adaptations which they exhibit.

15. *Ontogeny and Phylogeny of the Root*

Ontogenetically the root is a development from the tip of the hypocotyl, and its three principal functions are support, nutrition, and storage.

Phylogenetically the last word has not yet been said as to the origin of the root. Most botanists believe that living things originated in water. At first they were very simple, but as the ages passed they evolved into the groups of water plants which we call algæ. Certain kinds of algæ are familiar to everybody. Such are the bladder-wracks (*Fucus*) which cling in shaggy brown masses to the rocks exposed at low tide along the coast. Others are the devil's aprons (*Laminaria*) and the many red- and violet-colored forms which grow below the tide level. In fresh water too, occur many algæ, but all of them are green in color. One very common in stagnant water is called "frog-spittle."

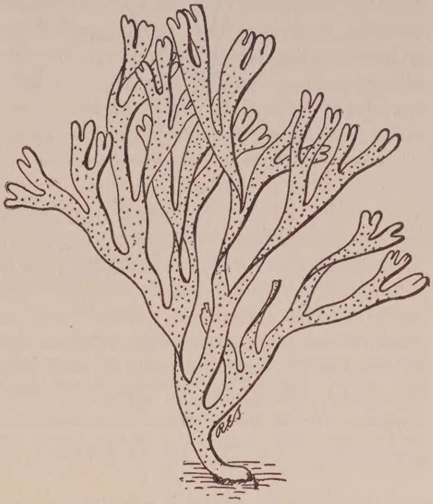

FIG. 7.— *Cutleria multifida*, a dichotomously branched thallus plant which may represent a form of body from which higher plants evolved.

The algæ are *thallus* plants, that is, plants without stems, roots, or leaves. They occur in bewildering variety, but the higher forms are often branched and ribbon-like (Fig. 7). As we have said, they probably constituted the earth's whole flora at one time. The lands in that ancient period were bare of vegetation, but as the ages rolled on, certain thallus plants migrated to the land and became the progenitors of the dry-land flora. One part of the thallus entered the earth and became a root; another part erected itself into a stem, while still other branches flattened out into leaves. Such a purely hypothetical transitional plant is shown in Fig. 8. Its reconstruction is based on a view advanced by Professor Lignier.*

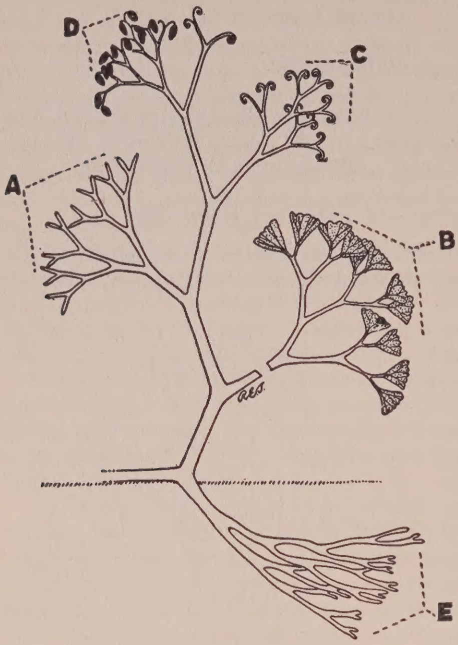

Fig. 8. — A Purely Hypothetical Primitive Land Plant Based on Lignier's Theory. Branch A is shown in its ancient algal condition; branch B has flattened out the tips of its branches to form leaflets (cf. certain ferns); branch C is like A, but in a young state with its tips coiled after the manner of many fern fronds as they unfold; branch D is shown as fertile and bearing sporangia; branch E has entered the soil and become a root.

It should be clearly realized that this view is only a hypothesis; we have not yet found any fossils of these transitional forms, though paleobotanical evidence accumulated within the last few years begins to attest the truth of a similar view.

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* This is the so-called homologous theory of the origin of land plants (O. Lignier, "Equisétales et Sphénophyllales, leur origine filicienne commune," *Bull. Soc. Linn. de Normandie*, 5th série, Vol. III, Caen, 1903). There is another view known as the *antithetic theory*, which is quite different. It would be impossible to explain the difference to the student at this point in his studies.

One thing is certain: "the root is the most conservative organ of plants," and retains a structure which we know stems also possessed in ancient days.

16. *The Three R's of Comparative Anatomy*

Professor Jeffrey has said that the three R's of comparative anatomy are *recapitulation*, *retention*, and *reversion*.*

You already understand the first — *recapitulation.*

We have just spoken of the second — *retention.* This means that certain parts of the plant's body may lag behind other parts in their evolution. In other words, certain parts retain archaic anatomical or histological features after other parts have given them up. The possession of endosperm by certain primitive *Leguminosæ* is a case of retention.

The third principle, *reversion*, has not yet been illustrated. It means, however, in botany, that when a plant is wounded, the new growth near the wound area will tend to show features characteristic of the ancestors. The hemlock has no pitch-canals in its stem or root wood, but the new growth made by a wounded hemlock may be filled with these canals. This fact, along with others, makes us believe that the pines were the ancestors of the hemlocks. The Greek word for wound is *trauma;* hence we often speak of traumatic stimuli and traumatic reversions.

17. *The Root in Botanical History*

Returning to the study of the root, we may note that it is an organ which in the older days of botany was considered very important. During the Renaissance period many books on plants were published. These books, called herbals, were lavishly illustrated with wood engravings and dealt mostly with plants which were useful (or at least supposed to be useful) in medicine. In every figure it will be seen that the root is very carefully drawn (Fig. 9). Yet we realize to-day that root features are of comparatively small value in the identification of plants. The reason for this emphasis on the root in the old herbals is not, however, difficult to explain, for it is the root which at certain seasons of the year stores up the food of the plant, and in it are concentrated the medicinal principles, many of which chemistry has been able to analyze and resynthesize. Hence, in the older medicine, the root was one of the most important parts of the plant. Think how many native plants have names relating to the root. Such are bloodroot, cancer-root, snakeroot, yellow-root, etc., names given by the old herb doctors.

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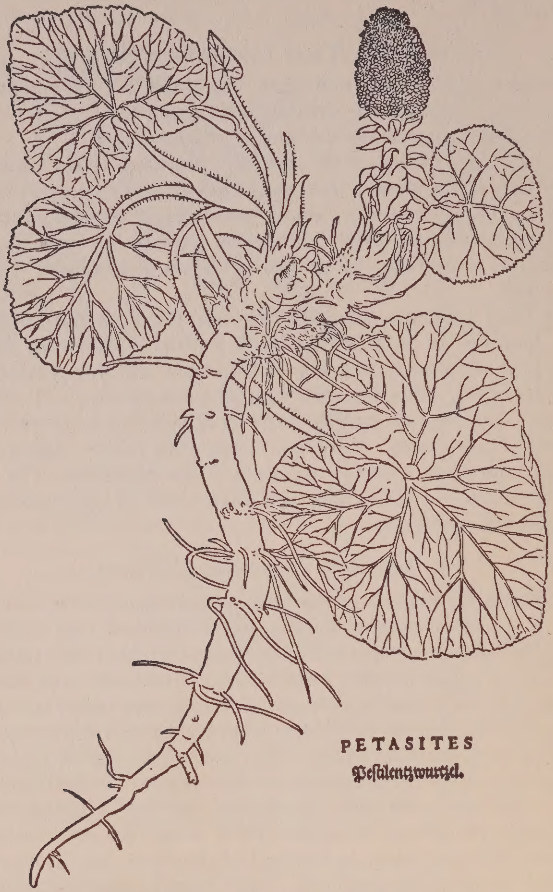
* E. C. Jeffrey, *The Anatomy of Woody Plants* (1917), Ch. 17.


PETASITES
Peſtilentzwurtzel.

"Petasites" = Butterbur [Fuchs, De historia stirpium, 1542]

Fig. 9. — A woodcut from Fuchs's herbal, showing how carefully the root is represented. (After Arber.)

18. *The Kinds of Roots*

A. NORMAL AND ADVENTITIOUS ROOTS

According to their place of origin, roots may be classified as either normal or adventitious. A *normal* root springs from the hypocotyl, and from it arise other roots and rootlets. *Adventitious* roots, on the contrary, arise from stems or leaves. On the ability of such parts to form roots and buds rests the whole horticultural practice of propagating plants by cuttings and layering. The horticulturist has a great advantage over the animal husbandryman in this respect, since he may, if he so desires, propagate any given plant almost indefinitely.

Plants with underground creeping stems are often well endowed with adventitious roots which spring from the nodes. Grasses are particularly well provided. If wheat, for example, be planted too deeply, the epicotyl elongates to carry the plumule out of the soil, and from its upper node adventitious roots arise and establish themselves at the distance below the surface of the soil which is conducive to the optimum air, warmth, and moisture requirements, while the primary root remains very small.

B. TAP-ROOTS AND FIBROUS ROOTS

Normal roots may be classified as either tap-roots or fibrous roots. In the origin of the former the primary root elongates and penetrates deeply into the ground, and the lateral or secondary roots do not particularly develop. Such elongated roots are called *tap-roots*, and they sometimes reach a remarkable length. The tap-root of the alfalfa may penetrate ten feet into the soil, and for this reason it is an excellent plant for dry-land farming, since it can reach moisture at low levels. A plant with long tap-roots is difficult to transplant, and it is often injured by successive freezings and thawings of the earth around it, since the heaving motion may break the root.

Sometimes a plant may seem to have several tap-roots. This is not uncommon in carrots and parsnips. The forking is due to the fact that several strong lateral roots have pushed out and have run down parallel to the primary root. This effect usually follows the death of the primary root-tip and is considered to be a manifestation of growth correlation. This means that the parts of a plant are so correlated that they work harmoniously together. If a part be lost, other parts attempt to make up for the deficiency and to restore the harmony. The same thing takes places in animals; if one kidney is removed, the other increases in size; if a man becomes blind, the senses of touch and hearing become more acute.

A *fibrous root* is one in which the main axis soon ceases to elongate and numerous lateral rootlets arise and branch vigorously. Fibrous roots are essentially feeding roots; they effectively explore the soil in all directions, and their total length is sometimes extraordinary (Fig. 10).* The root of an oat-plant measured in one instance over 450 feet in length, and yet it spread through little more than a cubic yard of soil.

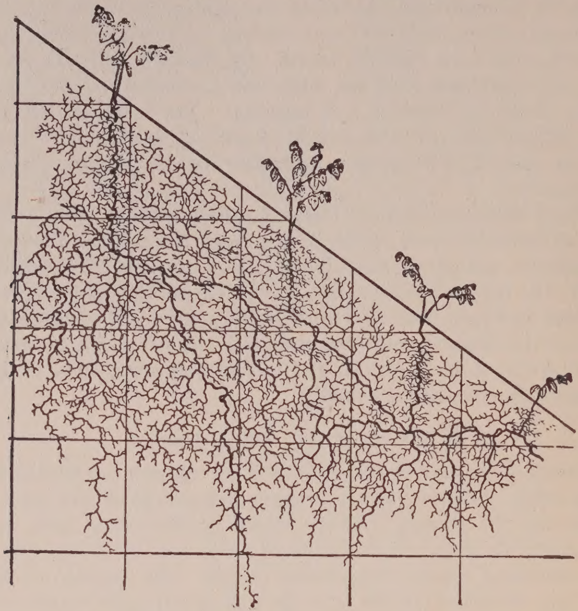


Fig. 10. — Drawing of the root system of the dogbane (*Apocynum androsæmifolium*), showing rhizomes and dense network of roots. The rulings mark off square feet. (After Weaver.)

Tree-roots sometimes enter wells or drain tiles and cause mischief. In the botanical museum of the Massachusetts State College is a specimen bearing this label:

> "Five-year-old pear-tree root taken from a drain tile. This root was responsible for clogging a 12-inch drain tile. It is five years old, 61 feet long, and the whole mass amounted to over two miles in length. The maximum number of roots in cross-section is 447. The root was single when it entered the tile."

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* See J. E. Weaver, *The Ecological Relations of Roots* (1919).

19. *The Relation of Roots to Soil*

It is practically impossible for a root to pursue a straight course through the soil; it is always meeting with obstructions. Some of these it pushes aside; others it grows around. Sometimes it enters a crevice between stones and becomes contorted or flattened through accommodating itself to its surroundings. It does not passively submit to such obstructions, however. The lifting power of a root is astonishing. There is a case on record of the root of a birch-tree which entered a crevice and lifted a boulder estimated to weigh twenty tons; this root was flattened like a ribbon, but it had succeeded in making some room for itself.

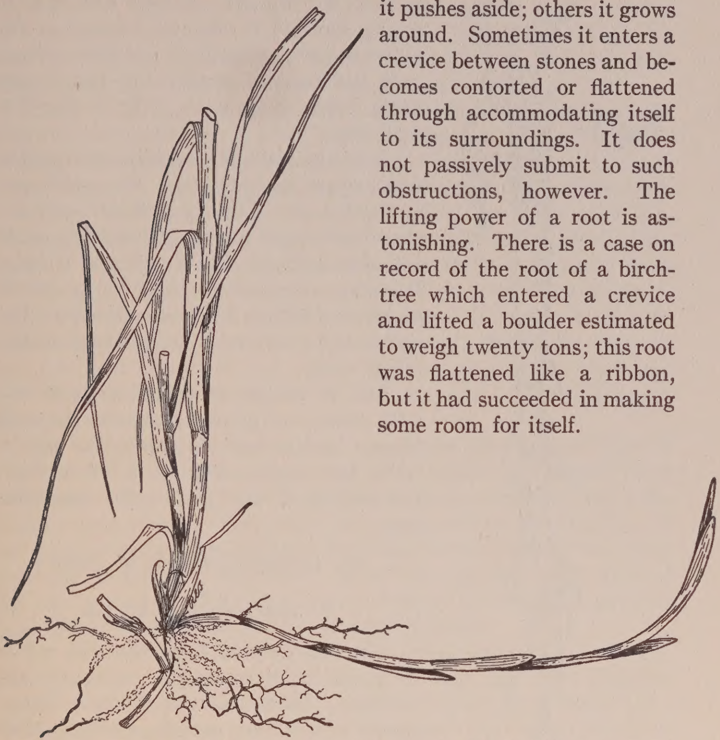

FIG. 11. — The Coastal Sand-Grass (*Ammophila arenaria*). The plant has crept upward through the sand and developed adventitious roots and a long stolon from an upper node.

We have said that the primary function of the root is to support the plant and supply it with water and food salts. Both these functions necessitate a widely ramifying system. This incidentally becomes a factor in geology, since roots are very efficient soil-binders. They prevent river banks from being eaten away so rapidly. In fact, willows which grow thriftily along stream banks are often planted to prevent soil wash. Again, the interlacing roots of forest trees prevent denudation of hillsides. Thoughtless deforestation sometimes produces dire results. Speaking of the soil destruction in the old fields of southern

Mississippi, Mc Gee says that they are washed away, "leaving mazes of pinnacles divided by a complex network of runnels glaring red toward the sun and sky in strong contrast to the rich verdure of the hillsides never deforested — whole villages once the home of wealth and luxury, are being swept away at the rate of acres for each year."

Roots may act as sand-binders along the coast where the sandgrass, *Ammophile arenaria* (Fig. 11), with its profusion of rootstocks and roots ties up the drifting sands and often initiates the formation of a dune. It is almost impossible to smother it, since if its base be buried, new roots arise from the upper nodes and so it keeps ahead of the piling sand.

Last of all, the interlaced roots of cattails, rushes, and grasses often form the basis of new land around the borders of ponds, lakes, and salt-marshes. It is the dead accumulations of such plants that constitute peat.

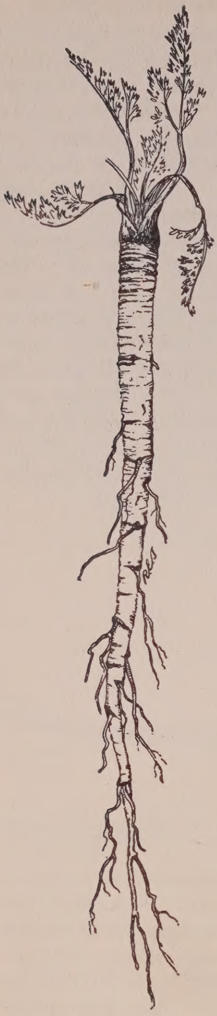

Fig. 12. — The Wild Carrot, Ancestor of the Modern Varieties of Cultivated Carrots.

20. *Ecological Forms of Roots*

A. STORAGE ADAPTATIONS

Thus far we have considered the root in its typical forms as adapted to support and nutrition. There is another function characteristic of the root, namely, storage. Most plants make more food in their bodies than is necessary for their immediate consumption, and hence the excess must be stored, to be used subsequently either for new growth or for the formation of seeds. All roots have the power to act as storage organs. The sap of many of our trees as it rises from the roots in the spring is filled with sugar. This was stored in the roots the preceding summer. As water begins to enter the roots from the thawing soil, the sugar is diluted and carried to the swelling buds. In the case of the maple the high percentage of sugar becomes of economic importance.

Sometimes the root becomes particularly adapted to the storage function, and it then takes on an inflated and swollen form. Among such roots are some of our most valuable root-vegetables such as the sweet potato, beet, carrot, parsnip, turnip, and radish. All such economic roots have been developed from wild ancestors.

In one of his fanciful tales, Jack London describes a group of our primitive, semi-intelligent, hairy ancestors leaving their caves in the morning to assemble in a wild carrot patch and feed on the "stringy-rooted carrots." Such a picture is possibly close to reality. Primitive man must have congregated where wild plant food was available. Then as his intelligence developed, he came to realize that plants grew better if cultivated, thinned, and kept free from weeds, and thus primitive agriculture arose. From this point it was but a step to planting seeds and growing a crop. So from the state of a wandering hunter he became an agriculturist, forced to settle down beside his crops, to wait for them to mature, and to live in harmony with his neighbors who were doing the same thing. So "society grew out of waiting for the crops to mature."

The varieties of plants we grow to-day are the result of what is called artificial selection. From the wild carrot, a common weed everywhere (Fig. 12), have been developed the numerous varieties of cultivated carrots. That this is true is proved by the fact that in the space of three years Vilmorin-Andrieux obtained roots "as fleshy and large as those of the garden carrot from the thin, wiry roots of the wild species." The carrot was introduced into English gardens from Holland during the reign of Queen Elizabeth.

By *artificial selection* we simply mean that seeds are taken year after year from specimens of plants which show the most desirable features. This finally establishes a pure line whose germ-plasm bears the desirable characters and which consequently will "come true from seed." Of recent years supplementary methods of increasing variation and of combining desirable characters from diverse strains have become possible through advance in the science of genetics.

Large storage-roots often characterize plants of arid regions. The great root of *Ipomœa pandurata*, a close relative of the sweet potato, may weigh as much as sixteen or even twenty-five pounds. The plant is a native of the Eastern United States. *I. leptophylla* (Fig. 13), the man-of-the-earth of the Western plains of Nebraska and Wyoming, attains a weight of 100 pounds and runs into the soil for four feet or more; it sometimes thrives where no rain has fallen for three years.

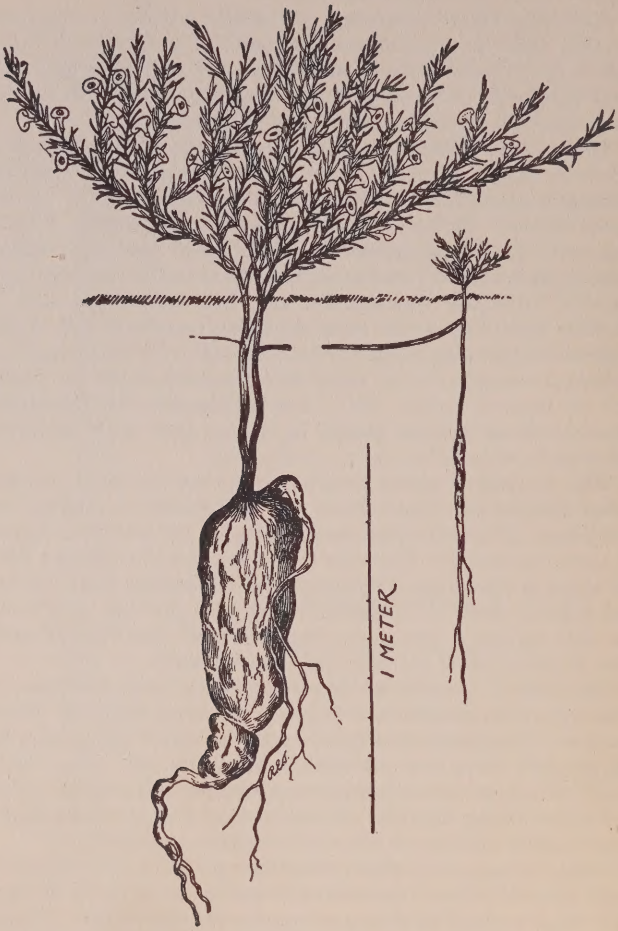

FIG. 13.—*Ipomœa leptophylla*, a Morning-Glory with Enormous Water and Food-Storage Root. (Redrawn from Morris.)

B. ANNUALS, BIENNIALS, AND PERENNIALS

Since the length of life of the plant depends on the length of life of the root, it may be seen that we have a basis here for dividing plants into annuals, biennials, and perennials. A typical *annual* lives but one year; during the growing season it manufactures food material and stores it in the stem; in the late summer it forms quantities of seed and transfers the stored food into endosperm. A typical *biennial*, like the carrot, lives two years. It devotes its first year to vegetative growth and the accumulation of food in a storage-root. Then its top dies. In the second year a new top arises from the crown and the food material is transferred into seeds. A typical *perennial* lives indefinitely, flowering and fruiting each year.

Climatic conditions seems largely to control the life period of a plant. In our gardens the castor-bean behaves as an annual; in the greenhouse and in tropical countries it is a perennial. If wheat be planted in autumn, it behaves as a biennial (winter wheat); if in spring, it grows as an annual (spring wheat).

C. PARASITIC ADAPTATIONS OF ROOTS

A remarkable adaptation of roots is seen in certain plants which become parasitic upon the roots or stems or leaves of other plants. Care should be taken to distinguish between *epiphytes*, *parasites*, and *saprophytes*. The lichens which live upon tree-trunks are merely epiphytes; they use the tree as a resting-place only. In tropical forests many plants seeking light become epiphytes and perch themselves high among the branches of trees. Particularly noteworthy are the orchids and the members of the pineapple family such as the Spanish moss (*Tillandsia usneoides*). Some small ferns and mosses actually become epiphyllous, that is, they fasten themselves to the leaves of tropical plants. We shall have more to say about the bodies of epiphytic plants later.

A *parasite* is a plant which lives upon another living plant known as its *host*, and by means of sucking organs robs its host plant of food; the mistletoe is a good example.

Saprophytes are plants which get their nutriment from decaying matter. Many fungi and bacteria and some flowering plants are saprophytes. A familiar example belonging to the last category is the Indian-pipe (*Monotropa uniflora*) of our rich woodlands.

Let us look more closely at a few parasites among our higher plants and particularly at the modifications which their roots have taken on to adapt them to their new life conditions. There are many grades of parasitism. Some parasites do most of their own work of food-making and are still green in color; they only enter into parasitic relations with roots of other plants which come in their way and are "to their taste." Such are our native cow-wheat (*Melampyrum lineare*), lousewort (*Pedicularis canadensis*), and bastard toadflax (*Comandra umbellata*).

(1) *The Cancer-roots and Balanophoras*

At the other extreme stand plants so highly specialized for parasitism that they have lost their chlorophyll and have reduced their leaves to colorless scales. Unless their seedlings succeed in finding a host plant they dry up and die. It is of interest to follow the life history of such a plant, and a species which is not uncommon with us, the one-flowered cancer-root (*Orobanche uniflora*), will serve as an example. As the embryo grows from the seed, its tip describes a spiral through the soil as if seeking a host. In case no host root is found, the seedling withers and dies; but if the search is successful, the root-tip of the orobanche glues itself tightly to the host root and swells into a flask-shaped tubercle (Fig. 14, B). Then the cotyledonary and hypocotyledonary portion of the embryo disappears, while from the tubercle arise many conical pegs (Fig. 14, C). At the point of attachment one of these penetrates the host root, passes through the bark, and inserts its own woody core so intimately among the woody strands of the host root that one cannot say where host begins and parasite ends. In fact, the union is so intimate that earlier botanists thought that the orobanche plants were pathological outgrowths from the hosts "produced from their tainted juices." Finally a scaly bud arises from the top of the tubercle (Fig. 14, D), and a flowering stem is sent into the air (Fig. 14, E).

A few orobanches get among cultivated plants and become of economic importance; *O. ramosa* attacks hemp and tobacco, while *O. minor* lives on the roots of clover-plants.

Among the most remarkable of all parasites are those uncanny tropical plants belonging to the families *Balanophoraceæ* and *Rafflesiaceæ*. The balanophoras live in dense tropical jungles; they are most brilliantly colored in shades of red, orange, or yellow and often have evil odors. One is called *Ichthyosoma* ("fish carcass"); another *Sarcophyte sanguinea* ("bloody flesh plant"). Like the orobanches, these plants form ball-like swellings on the roots of trees and plunge their sucking roots into the wood of their host.

The balanophoras may be used to illustrate an old belief which played a prominent part in the medical lore of the Middle Ages. Along the Mediterranean grows a member of the family called *Cynomorium coccineum;* it is blood-red in color and has a red juice. In the Middle

Ages it was taught that God had created all plants for man's use, and in order that man might know for what use each plant was intended, God had set a mark or "signature" on it. This was the "doctrine of signatures." A plant whose leaves had three lobes and which bore a fancied resemblance to the liver must be a cure for liver troubles; our spring-flowering hepatica received its name from this supposed virtue (Fig. 15, A). The belief in the doctrine of signatures still survives among backward people. The Chinese will pay high prices for ginseng roots with two prongs which recall the legs of a man, the idea

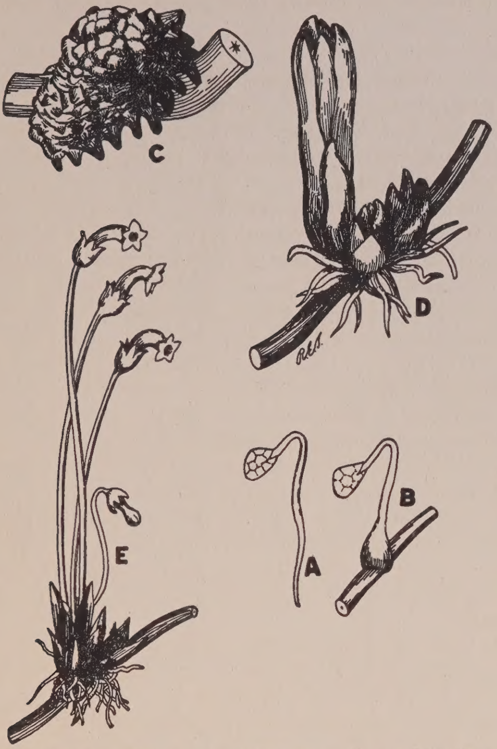

FIG. 14.—The One-Flowered Cancer-Root (*Orobanche uniflora*) and Its History from the Seed: A, germinating seed; B, production of primary parasitic tubercle; C, later stage (magnified) with primary tubercle producing many peg-like parasitic roots; D, vegetative stems and buds arising from the tubercle; E, flowering plants. (A, B, C, D, adapted from various authors.)

being that these "man-roots" are potent medicines. In the Middle Ages the mandrake (*Mandragora*) had the same reputation, and many weird tales were told about the plant: that its root was shaped like a man; that it would cry out when pulled from the earth. It is said that herb-vendors would attach wooden heads and arms to the roots and sell them to the gullible peasants in country districts.

The blood-red *Cynomorium* (Fig. 15, B) of which we have spoken was venerated as a styptic. For had God not shown, by giving it blood for its juice, that it was to be used for stanching the flow of blood? The dried plant was sold in apothecary shops under the name of "*fungus Melitensis*," since much of it came from Malta. Besides its styptic properties it was believed to have many other miraculous virtues.

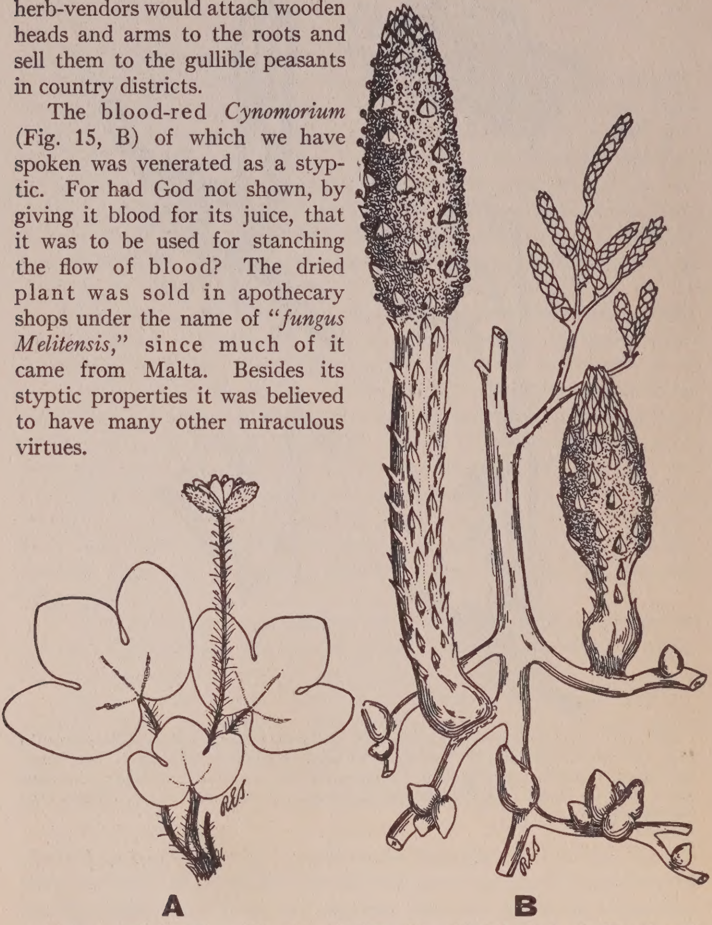

FIG. 15. — A, *Hepatica triloba*, Once Used as a Liver Medicine under the Teaching of the "Doctrine of Signatures."

B, *Cynomorium coccineum* ("*fungus Melitensis*") Growing as a Parasite on a Salicornia Plant. (Adapted from Kerner.)

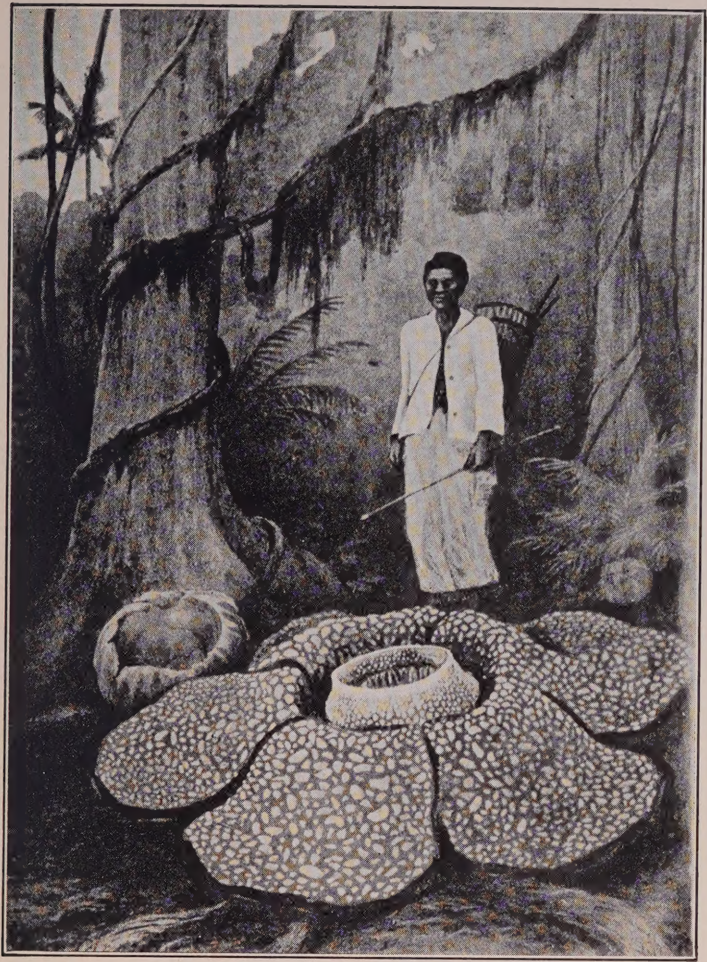

FIG. 16. — *Rafflesia Arnoldi*, a Parasite Which Bears the Largest Known Flower, Measuring Three to Five Feet in Diameter. (After Mitra.)

(2) *The Largest Flower on Earth.*

Most wonderful of all parasites is *Rafflesia Arnoldi* (Fig. 16). It grows only in the jungles of Sumatra and is parasitic on the roots of a tree (*Cissus sp.*). First to appear above the soil is a great scaly bud which resembles a red cabbage; this expands into a flower three to five feet in diameter and weighing about sixteen pounds. It is orange in color, is marked with yellow spots, and has an evil odor. It is believed to be spread by elephants which carry the seeds on their feet.

(3) *The Mistletoe.*

Not all parasites depend on the root of the host plant for their food; many live on the stems or even the leaves of their host. We have already mentioned the mistletoe, which is a stem parasite. The American mistletoe (*Phoradendron flavescens*) is very common on branches of trees in the Central and Southern United States, though the life history of the European mistletoe (*Viscum album*) is better known (Fig. 17, A).

Birds eat the fruit and the seeds are deposited in their excrement on the branches of trees. The seeds germinate, and no matter in what direction the micropyle may be pointed, the hypocotyl curves toward the branch and upon reaching it flattens out into an appressed disc. From the under side of the disc a spike-like root called a *sinker* develops. It pierces the bark of the host and runs down to the woody core, but never enters it. As the host branch grows in thickness by the addition of annual rings of wood, the tip of the sinker is sealed in, but it begins to elongate above and thus keeps ahead of its host. In its elongating region, however, just on the outer face of the wood, the sinker produces lateral roots which creep upward and downward beneath the bark and send in sinkers in their turn. They also give rise to adventitious buds from which new branches develop. Thus the root system of an old mistletoe plant comes to look like a rake driven into the tree. The teeth of the rake are the numerous sinkers, while the cross-bar corresponds to the creeping root itself from which the sinkers arise (Fig. 17, B). As the lateral roots and new sinkers develop, the aërial part of the plant increases in size. In cases where food is abundant, an old mistletoe plant may be four meters in circumference with an axis five centimeters thick. Attempts to extirpate it by cutting it away only make more trouble since the lateral creeping roots which lie under the bark proceed to send up crowds of adventitious branches. In some parts of Europe the mistletoe is a troublesome pest on apple-trees.

(4) *The Dodder.*

As an example of another stem parasite which has become very degenerate and has entirely lost its chlorophyll we may consider the dodder (*Cuscuta*, Fig. 18). This plant is a familiar sight in summer; it grows along moist country roadsides and along river and stream banks, producing stunted patches of vegetation intertwined with a tangle of its orange-colored threads. If one unwinds a single thread from a host plant it is evident that the parasite is attached by boring suckers; these are really highly modified adventitious roots. The

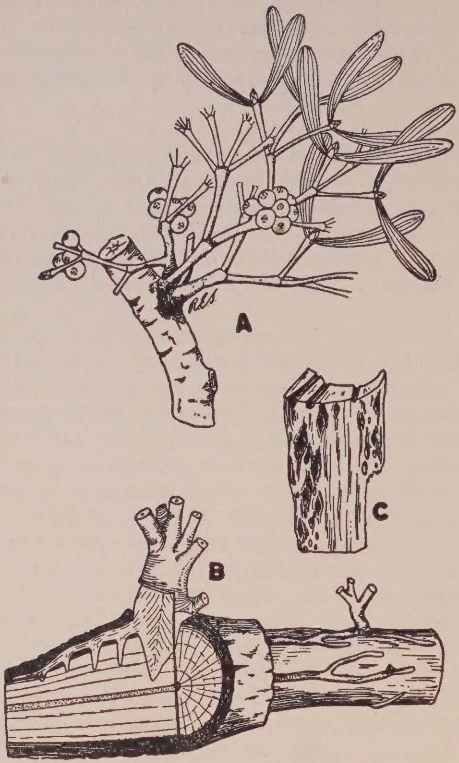

FIG. 17. — The European Mistletoe (*Viscum album*): A, mistletoe plant parasitic on a tree-branch; B, host branch split open (left) and decorticated (right) to show relation of parasite to host; C, piece of dead host branch from which the mistletoe "sinkers" have decayed. (Adapted from Kerner and from France.)

dodder has a peculiar life history. The following description is adapted from Kerner*:

The seeds germinate about a month later than those of other plants; this assures a good supply of host plants in the neighborhood. The embryo is undifferentiated, but the hypocotylar end issues first from the seed and fixes itself in the soil by its abortive root. The cotyledonary end, with the seed, pushes upward, and the median part of the embryo begins to elongate. By the fifth day the entire embryo has increased its length four-fold. After the endosperm is wholly absorbed, the testa is thrown off and the young plant is cast on its own resources. Having no chlorophyll, it cannot manufacture food, though it can get water through its basal end. The hypocotyl soon begins to shrivel. If the upper part of the seedling now touches the stem of a plant which can serve as a host, it is safe, and straightway coils itself tightly about it and sends in sucking roots. Suppose, however, that no host is available — then the seedling falls over on the earth due to the death of its hypocotyl. It may lie there alive for four to five weeks. Very rarely does it miss out in this period of "watchful waiting," for ultimately a growing shoot is almost sure to touch it. In this event it seizes the anchor thus thrown out, winds itself around it with a few close coils, and sends in sucking roots. Its tip then becomes free and begins to rotate in a circle like the hand of a watch. This activity brings it in contact with other plants and in this way the parasite spreads from place to place. It is now wholly unconnected with the earth, but in the fact that it possesses an abortive first root we can see another example of the biogenetic law. If the seeking tip of a growing dodder-plant happens to wind around a dead support, the stubby roots merely flatten out into holdfasts.

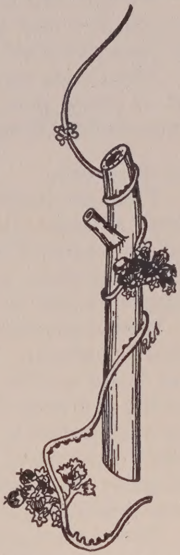

FIG. 18. — *Cuscuta Gronovii*, the Dodder, Parasitic on a Stem of jewel weed.

Certain species of dodder are destructive parasites; *Cuscuta Epithymum* sometimes attacks clover and is spread with clover seed from infected fields. *C. Epilinum*, the flax dodder, is very injurious to flax in Europe. Both these species have gotten into the United States. *C. europea* sometimes ravages hop plantations; it is the most widespread of all the species, ranging from England to Japan and as far south as Algiers. It has been found once in Maine on native vegetation.

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* A. Kerner, trans. F. W. Oliver, *The Natural History of Plants*, 2 vols. (1902).

D. AËRIAL ROOTS

Up to this point we have spoken of roots which typically enter the soil or other substratum and serve for support, nutrition, and storage.

We may now take up a few root forms which arise freely in air, though they may later enter the earth, for the distinction between air roots and other types is not a sharp one.

Aërial roots may be classified rather arbitrarily into those which act as props, those which serve for climbing, and those adapted to water-absorption and food-making.

(1) *Prop-roots.*

These are familiar to all, since they occur at the base of strong plants of Indian corn. They arise in whorls at the lower nodes and radiate downward into the soil. Their obvious use is to prop up the tall, slender plant, but after entering the soil they not only serve as attachment organs but take on the feeding function as well.

Some tropical plants have striking prop-roots. Such are the screw-pines (*Pandanus*). In many cases the main stem of this plant dies and decays and the plant is left to rest on its prop-roots alone, appearing as if elevated on stilts. The mangrove (*Rhizophora*, Fig. 19), has a similar habit. Its many branching prop-roots form a profuse tangle in the coastal swamps where it grows. In addition to these the mangrove also possesses a system of props of the same nature as those described in the next paragraph.

Closely allied to prop-roots are those which descend vertically from the branches of various trees of the genus *Ficus*. One of these is *Ficus bengalensis*, the famous banyan-tree of India. From its spreading branches descend aërial roots which upon reaching the soil become fastened as nourishing roots. As they thicken with age they act as props to the branches, which are thus enabled to spread out over a wide area. In the Botanic Garden of Calcutta there is a banyan-tree about 100 years old whose main trunk some years ago was forty-two feet in circumference, while 232 additional trunks, many of them eight to ten feet around, carried the branches outward over an area 850 feet in circumstance. The banyan-tree under which Alexander is reputed to have camped 7,000 men is now 2,000 feet in circumference and has 3,000 trunks.

(2) *Climbing Roots.*

Special roots which spring from the stems of plants and affix themselves to trees and walls are not uncommon. The poison-ivy (*Rhus*

Toxicodendron) climbs in this way, as does also the English ivy (*Hedera Helix*, Fig. 20), and the trumpet creeper (*Tecoma radicans*). Sometimes such roots will enter pockets of moist soil and turn into absorptive organs, but in other cases they have entirely lost their normal root functions. Some species of climbing figs, closely allied to the banyan-tree, produce great quantities of climbing roots which may finally strangle and kill the tree to which they cling.

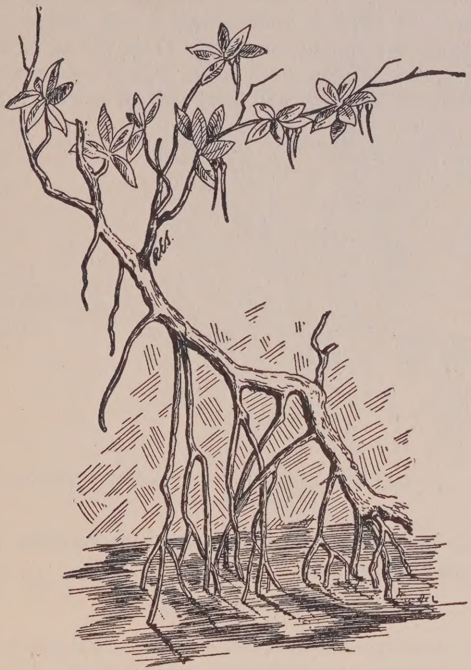

FIG. 19. — The Mangrove (*Rhizophora conjugata*) Advancing into the Sea by Means of its Prop-roots. (Adapted from Kerner.)

(3) *Air Roots Adapted to Water-absorption and Food-making.*

We have spoken already of the epiphytic orchids and aroids which perch themselves on trees in tropical forests. Most of them produce a special kind of air root (Fig. 21). These are covered with a sheath known as a *velamen*, underneath which is a layer of green bark. Consequently such roots not only absorb moisture but they can also manufacture food as a leaf does. Most remarkable of all orchids from this standpoint is *Tæniophyllum*, a plant without leaf or stem, the flattened and branching green roots of which make up the whole body.

(4) *Root Knees.*

One more root type demands mention. This is well seen in the bald cypress (*Taxodium distichum*) of the Southern United States and is called a *pneumatophore* or cypress knee. The bald cypress grows in swamps where the water is undoubtedly low in oxygen content and perhaps charged with deleterious gases. From the subterranean roots which ramify through the muck arise curious columnar or conical bodies. Their bark is spongy and filled with air spaces. It is generally believed that they absorb air and conduct it to the parts of the plant which lie buried in the mud.

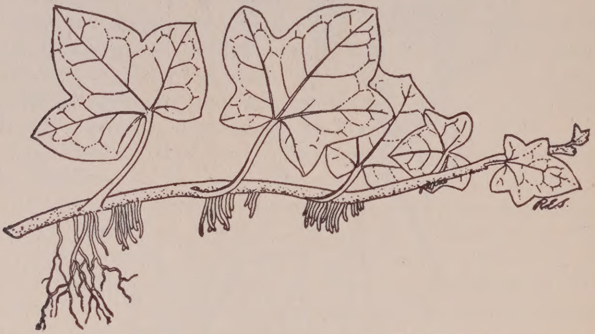

FIG. 20. — The English Ivy (*Hedera Helix*), a Vine Which Climbs by Means of Adventitious Roots.

21. *Summary*

We may close our study of the root with a rapid summary.

The root is an organ which arises ontogenetically from the tip of the hypocotyl; phylogenetically it may have been derived from a subterranean branch of some ancient dichotomizing thallus plant. It has the primitive structure which characterizes ancient stems and seems to illustrate the principle of anatomical retention.

Roots may be divided into normal and adventitious, and into tap and fibrous roots; the latter are often remarkably developed as a feeding system. The primal root functions are support, absorption, and storage. The first function makes them important soil-binders. Deviations from the fundamental type lead to ecological adaptations to storage (root crops); to parasitism (orobanches, balanophoras, *Rafflesia*, mistletoe, dodder); to service as props and buttresses (corn, screw-pines, mangroves, banyans); to climbing (ivies, trumpet creepers, etc.), and to air conduction (pneumatophores of bald cypress and mangroves).

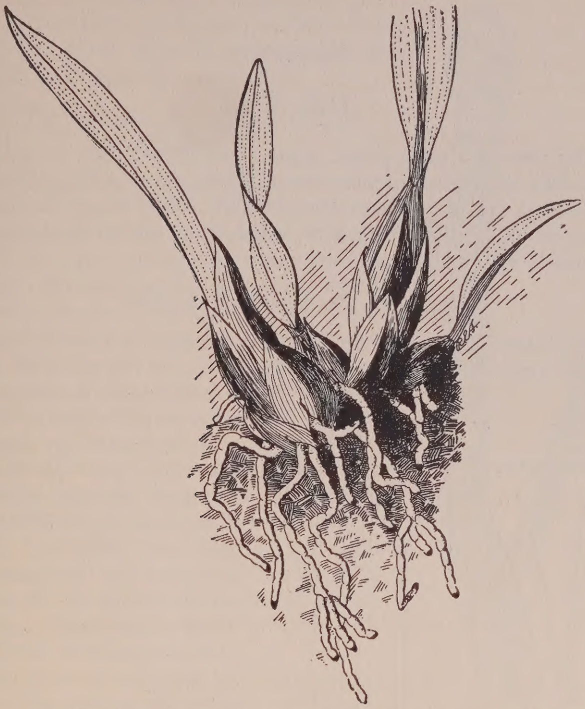

FIG. 21. — An Orchid Plant Bearing Adventitious Aërial Roots Which Absorb Water and Also Manufacture Food.

CHAPTER IV

THE STEM

The stem is a more plastic organ than the root, and its ecological variations are much more numerous. This probably depends in part on the fact that the stem is more strongly subjected to the forces of the environment than is the root, which in its subterranean life finds conditions very uniform.

22. *The Phylogeny of the Stem*

Phylogenetically the stem, like the root, may be a derivative of an ancient algal thallus, but in the case of the stem there is some actual paleontological evidence which bears on the subject.

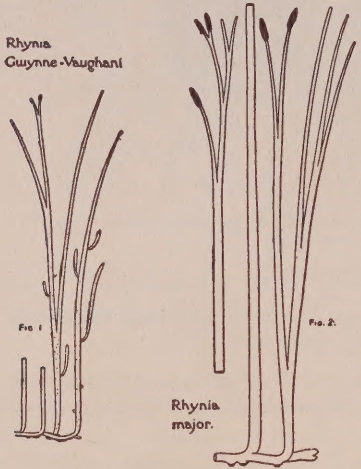

FIG. 22. — Reconstructions of Two of the Most Ancient Land Plants from the Devonian Period. They are leafless and rootless. (After Kidston and Lang.)

A few years ago there was discovered near the town of Rhynie in Scotland, in deposits of Devonian age, beds of silicified peat made up almost wholly of the small stems of certain plants new to science. These plants caused a considerable sensation in the botanical world, for not only are they the most ancient land plants known but they are without roots, while two genera, *Rhynia* and *Hornea*, are also without leaves (Fig. 22). They consist, then, wholly of slender stems which branch dichotomously and bear spore-sacs at the tips of the branches. They are small plants — some eight inches tall and only one-fourth inch in diameter in their main stems. Their rootless bases were fixed to the soil by delicate hairs such as occur to-day on mosses.

These queer plants certainly suggest a derivation from some such dichotomously branching green algal thallus as is hypothesized by Professor Lignier, and it looks as if we had caught such a plant in its transition state from water to land before it had evolved roots and leaves. If these inferences are correct, then the stem is phylogenetically older than the root or leaf.

23. *The Woody Stem in Its Winter Condition*

In Chapter I we studied the stem of an herbaceous plant. Such a stem, however, is less typical of the organ than that of a woody type, and among woody stems none is better for an introductory study than that of the horse-chestnut (Fig. 23).

If we examine a rather slow-growing twig of the horse-chestnut in its winter condition, it is at once evident that it differs considerably from the herbaceous stem. It is coated exteriorly with gray or brown cork whose chief function is to prevent the evaporation of water from the twig. It is particularly serviceable in winter when the roots cannot absorb water from the frozen soil and hence the danger of fatal desiccation is great. The cork is pierced with small breaks called *lenticels*, and this still permits the interchange of gases with the outer air.

The most conspicuous features of such a resting branch are the brown, scaly, resin-coated buds. The largest of these are the terminal buds which by their subsequent growth will lengthen the branch; the smaller are the lateral buds which stand just above horseshoe-shaped scars and are placed opposite one another. Their development will bring about the production of lateral branches. The position of the buds leads us to infer that the large scars beneath them are leaf scars left by the falling of the petioles the preceding autumn, while the small points on the scars, comparable to the nails of a horseshoe, can only be the broken ends of the leaf-traces which formerly ran through the petiole.

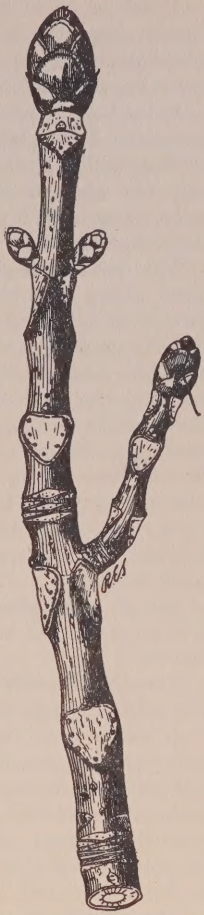

FIG. 23. — Branch of the Horse-chestnut (*Æsculus Hippocastanum*) in the Winter Condition.

The horse-chestnut leaf possesses seven leaflets, and the ends of seven leaf-traces are to be seen on the scar.

It will be noted that the pair of buds at the next node alternates with the first, that is, if the first pair is directed north and south, the second faces east and west. This, of course, prevents the shading of one pair of leaves by another and distributes their weight more evenly.

If the branch is more than one year old, it will bear certain narrow corrugated bands between the successive yearly growths. These bands are called *girdles*, and it is not difficult to understand how they arise. For when the terminal bud pushes out in the spring, the brown scales, being of no further use, are cast off and leave a girdle of clean scars behind them.

The question of the morphology of the bud scales may now be raised. They lie in alternating pairs even as do the true leaves, and when they fall away leaf-trace markings are visible on their scars. This can only mean that they are curiously modified leaves and that some half-dozen nodes are closely crowded together at the girdle. But if the bud scales are leaves, what part of a leaf do they represent? They look like leaf blades, and the inner green ones will be found to simulate blades even more than the outer. Sometimes, however, at the very base of a bud the outermost scales will be found to bear tiny spurs at their tips, while in the growing season this tip may even bear a few rudimentary leaflets. The bud scale, then, must really be a flattened and concave petiolar base, not a blade, as a hasty glance would suggest.

Not all bud scales, however, are petiolar; those of the lilac are derived from the leaf blade, while those of the tulip-tree are modified stipules.

Though the study of bud anatomy belongs more properly to the next chapter, yet we may introduce it logically at this point.

It will be noted that the scales lap over one another in much the same way as do the shingles on a house. They are said to be *imbricated* (*imbricare* = "to cover with tiles"). Inside the scales will be found a small stem beset with several miniature horse-chestnut leaves densely swathed with wool. If the bud is a strong terminal one, a cluster of flower-buds may also be enclosed. Thus all is prepared and waiting for the sudden rush of growth which will come with the spring. To see just what does happen normally in spring we need only place the shoot in water in a warm place. The inner parts begin to swell, and the bud bursts open. The new stem elongates, the young leaves increase in size, unfold, and turn green. The wool (highly developed pubescence) falls off in tufts. The inner bud scales enlarge slightly but finally all fall away, leaving a new girdle of scars.

When forced in water in this way the soft parts soon die, since only the small amount of food stored in the stem and bud itself are available for growth.

The natural destiny of all buds is to develop into branches the succeeding season, but an examination of almost any branch shows that many of the lower buds remain in a resting condition. The advantages to the plant of thus possessing dormant or resting buds are several. First of all, if the terminal part of the twig is killed, the resting buds may then push out into activity; again, if all the buds were to grow, the congestion of branches would interfere with their optimum efficiency. In addition to the *normal buds*, namely, those which are associated with leaves, many plants develop *adventitious buds* just as they develop adventitious roots. These are often correlated with traumatic stimuli, and very commonly a tree which has been severely pruned will develop numerous adventitious buds which may grow out into the familiar "water-sprouts." The phenomenon known as a witch's broom, in which hundreds of small twigs grow from a localized area of a stem, is due to some traumatic disturbance set up by fungus or insect parasites. Adventitious buds are not necessarily confined to stems; they may appear also on the roots and leaves of some plants.

The horse-chestnut possesses a type of winter bud which is common among trees of northern regions. Some buds, however, are not protected by scales at all but have their small leaves merely folded tightly upon one another. Such are called *naked buds;* they are, of course, characteristic of tropical trees and undoubtedly represent the original bud condition of all trees.

24. *Paleoclimatology and the Deciduous Habit*

Several broad and interesting topics may be naturally associated with the study just completed.

The horse-chestnut stem is obviously remarkably adapted to winter conditions: its leaves have fallen away; its surface is covered with cork; its buds are scale-covered, waterproofed, and wrapped in wool. We can realize that it is a structure which must represent the culmination of a long antecedent evolution. Fortunately we know a part of the explanatory facts and we can infer the rest. We know that in the Cretaceous Period eternal summer reigned over the whole earth. In Greenland and Alaska, and even to within a few degrees of the North Pole itself, a rich forest flora covered the lands and spread away southward to Graham Land near the South Pole. And more remarkable still, palms, breadfruits, figs, and other tropical trees grew intermingled with pines, oaks, beeches, and willows. There was no winter and no resting season; the trees must have shed their old leaves a few at a time just as the tropical trees do to-day.

What brought on the Ice Age we do not know, but as the northern lands began to cool, the plants and animals were forced southward. In the antecedent refrigeration which preceded the Glacial Period there came a sorting-out of the ancient flora. Those plants which could best stand the encroaching cold remained in high latitudes; those which could not were driven toward the equator and finally shut into the equatorial belt where we find them to-day.

We are still very close to the Glacial Period — in fact it is by no means certain that the ice will not one day descend again. Already geologists have recognized four of its minor pulsations and retreats. During these mild interglacial periods the plants pushed northward, some of them even beyond their present range.

Before the Glacial Period there seem to have been far fewer herbaceous plants on earth than to-day; instead, trees dominated the floras. To-day the tree flora is on the decrease, and herbs threaten to dominate the earth eventually. As the ice crept down, the trees slowly adapted themselves to the recurrent winter season; they learned to cast off their foliage, to develop a protective cork jacket, and to transform certain of their leaves into bud scales.

In relation to the origin of the deciduous habit it is of interest to consider the oak. Oaks are tardily deciduous in the fall, and it has been noted that young oaks retain their leaves long after the adults have lost them. In the Southern United States grow a number of species known as "live-oaks" because of their evergreen habits, and there is paleobotanical evidence that the live-oaks formerly ran far northward. These facts suggest that the ancient oaks were all evergreens and that the tardy shedding of leaves in the fall is an instance of partial retention of an archaic character. If this be true, the young oaks evidently illustrate recapitulation and the live-oaks are merely persistent primitive types.

The great physiological value of the deciduous habit is that it checks evaporation of water from the plant. We have seen, too, that the bud is protected by scales and waterproofed with resin for a similar reason. Such features must have taken ages to evolve, and we may infer from the plants themselves, as geology also teaches, that the oncoming of the Ice Age was a very slow process.

25. *Functions of the Stem*

Turning again to the study of the stem, we may inquire as to its basic functions. These in general are (1) to hold the leaves so that they may be most advantageously related to the light; (2) to manufacture food; (3) to serve as a storehouse for food even as does the root; (4) to act as a channel of communication between root and leaves.

A. ADAPTATIONS TO THE LIGHT RELATION

As has already been explained, green plants are absolutely dependent on light as the source of energy with which they can manufacture food. The green parts being sun-engines, it becomes of supreme importance that the leaves should be adjusted in such a way as to receive the optimum illumination. In the case of a typical stem evenly illuminated from all sides, it is obvious that a spiral distribution will be particularly advantageous.

(1) *Phyllotaxy.*

Suppose we examine a straight leafy twig of the common swamp alder (*Alnus incana*). Since, as we have seen, an axillary bud always marks the position of a leaf, a twig in its winter state will do as well. Starting with any chosen bud it will be found that the next one upward stands 120° away from the first or one-third the distance around the stem. Continuing upward we find that the next is placed 120° from the second, or 240° from the first, while number 4 stands directly above number 1 and completes the spiral. The arrangement of leaves on the stem is called the *phyllotaxy* and the alder is said to possess the 1/3 phyllotaxy. In this fraction the numerator represents the number of turns around the stem necessary to bring another leaf directly above the first, while the denominator represents the number of leaves passed through in making the turns.

If instead of an alder twig we choose the twig of the apple, it will be found that the phyllotaxy is 2/5. In other words, in passing from any leaf to the one directly above it, the spiral is obliged to circle the stem twice and to cut the bases of five leaves.

The next higher phyllotaxy above the 2/5 is the 3/8, the next 5/13. It will be observed that the successive phyllotaxies form a series (1/2, 1/3, 2/5, 3/8, 5/13, 8/21, 13/34) . . . the successive terms of which consist of the sum of the numerators and denominators of each of the two preceding terms. The higher phyllotaxies are rare. By far the most common is the 2/5. The 3/8 arrangement occurs in holly and in the root leaves of the plantain. The 5/13 is found in the cone of the white pine, while in a certain fossil plant (*Lepidodendron*) a phyllotaxy represented by 89/233 has been worked out.

Whatever the underlying basis of such natural mathematics may be, the practical result is the distribution of the leaves in such a way that any one receives the maximum amount of light with the minimum of shading by leaves higher up on the stem. Other adaptations of the leaf itself conducive to the same end will be described in the next chapter.

(2) *Special Adaptations of Stems to Leaf Display.*

In adapting themselves to the light relation many stems have departed widely from the typical upright conditions. Certain plants have a weeping habit of growth; their long, flexuous branches spread outward and downward like a fountain, and under these conditions, too, the leaves usually face outward — a state which is brought about by torsion of the petioles.

a. Trailing stems. Stems often become elongated and trailing, and the leaves are twisted to the upper side. This habit is of considerable advantage to the plant, since first of all it enables the plant to dispense with the mechanical supporting tissues to the construction of which upright stems must devote so much food and energy. Furthermore, it is a protective device, since the extremes of heat and dryness are less active near the soil. Last of all, it is a reproductive device, for such trailing plants usually root at the successive nodes, and the death of the parent merely isolates a group of branches which subsequently assume an independent life. It is an axiom of morphology that all dorsiventrality is secondary; viz., the creeping habit is not a primary condition for any plant.

b. Climbers and lianas. Instead of trailing along the earth, stems may become scramblers over walls or stumps, or over other plants. They are often assisted by hooked thorns or by tendrils in maintaining their hold on such supports. Particularly noteworthy are the climbing palms known as rattans, which by means of their spiny leaves may climb to the tops of tall trees and even loop from one tree to another. Rattan stems 200 meters long with a diameter of only two to four centimeters have been reported.

A general term for such woody vines is *lianas* or *lianes;* they are abundant in the tropics — in fact, Kerner estimates that there exist some 2,000 species of such plants. Speaking of the tropical forest he says:

> "This is the true and proper home of the liane. Everything climbs, winds and twines with everything else, and the eye in vain attempts to ascertain which stems, which foliage, which flowers and fruits belong to which. Where the lianes have grown old with the trees on which they cling, and the older portions of their stems have been long stripped of foliage, they resemble ropes stretched between the ground and tree-summits, and often assume peculiar and characteristic forms. Sometimes drawn out tightly, sometimes limp and swaying, they rise up from the undergrowth of the forest ground and become entangled and lost far above among the boughs. Many are twisted

like the strands of a cable, others are wound like a corkscrew; and others again are flattened like ribbons, hollowed in pits, or shaped into elegant steps — the celebrated monkey-ladders."

c. Twining stems. Highest in the category of vines must be placed the twiners. A twining plant begins life in the regulation manner as an upright seedling, but as it grows older its elongate and flexuous upper part begins to describe an ellipse or a circle. The movement may be simulated by holding a flexible carriage whip above the head and whirling its upper part. It naturally follows that if the moving tip of the plant comes into contact with a small cylindrical support, the stem will wind around it. The rotation movement of the tip is rather rapid; the tip of a hop stem in warm weather makes the circuit in two hours and eight minutes; that of *Akebia quinata,* a Japanese vine, in one hour and thirty-eight minutes; while in *Grammatocarpus volubilis,* a climber from Chile, it is accomplished in one hour and seventeen minutes.

All stem tips advancing upward do so in an irregular manner, bending now one way, now another, in movements which are called *nutations.* The twining motion is probably a specialization of this normal movement; it is called by the special name of *circumnutation.* The direct cause of the movement seems to be the advancing of a regular zone of contraction around the stem which causes it to nod always toward the contracting side, the summation of the nodding movements bringing about a circular sweep.

Some twiners move in a clockwise direction, viz., from the east through the south toward the west; these are called *dextrorse climbers.* Others turn east, north, west in a counter-clockwise direction and are called *sinistrorse climbers.* Hop and honeysuckle are dextrorse, while the scarlet runner bean and the Dutchman's pipe vine are sinistrorse. We may speak of them as right-handed or left-handed climbers.

d. Tendrils. To assist the main stem in getting into the air certain plants have developed their lateral axes into special gripping organs called *tendrils.* The grape family offers us a specially interesting series, for in this case the tendril seems to have been derived from a flower cluster, and a flower cluster is only a system of lateral branches rising from a leaf axil.

In the Boston ivy (*Psedera tricuspidata,* Fig. 24), which climbs over plain brick walls, the first modification of the inflorescence to fit it for the climbing function may be observed. If we examine the young growing tip of a branch, it will be found that rising from certain leaf axils are slender branching organs whose ultimate tips are swollen into small knobs. If these be observed from day to day, they can be seen to apply themselves to the bricks and there to flatten out into discs ("just like the toes of a tree-frog"), which glue themselves so tightly that they will break before they will let go their hold. The pads of this *cirrhus*, as the whole structure is called, are actually modified parts of a flower — small abortive grapes which have taken on the curious function of adhesion to bare surfaces.

In another member of the grape family (*Psedera inserta*), the young tips penetrate small crevices and then swell out and fit themselves so intimately to the contours of the cavity that when they are removed by dissolving the rock around them by chemical means, it is found that their surface is impressed with every tiny mark much as sealing wax would be if it had been forced when fluid into the crevice.

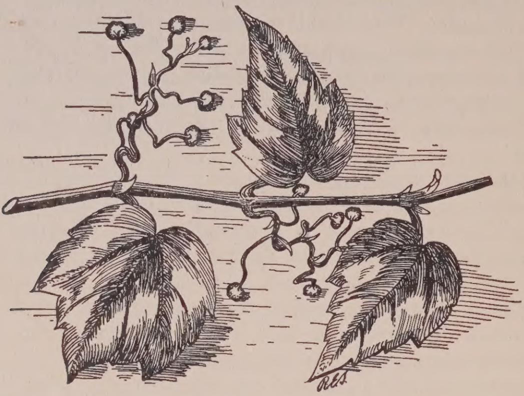

FIG. 24. — The Boston Ivy (*Psedera tricuspidata*) with Climbing Cirrhi (Modified Inflorescences).

The tendril of the grape (Fig. 25) exhibits a different modification. That the grape tendril is also homologous with the axis of a flower cluster is proved by the fact that grapes are very rarely borne on a tendril. A young tendril behaves much like the tip of a twining stem — revolving in a circle till it reaches a support, to which it grips firmly and about which it winds. The remarkable sensitivity of tendrils to contact has long been a source of remark. The tendril is only stimulated to coil when it contacts the uneven surface of a solid body; rain-water, or even the shock of a continued fall of mercury drops, produces no motion. If a glass rod be covered with gelatin and rubbed upon the tendril, no motion ensues; but if a film of butter be spread over the gelatin and the tendril be touched ever so lightly, it responds at once, since the butter contains tiny salt crystals. It has been found that a fiber of cotton weighing .00025 milligram is sufficient to cause the bending of a tendril.

e. Stemless plants and rosettes. At the other extreme from the elongated and flexuous stem adapted to leaf exposure comes the so-called stemless or acaulescent plant. To this category belong the dandelion, plantain, etc. It is evident that the term *acaulescent* is really a misnomer, for a stem is present, though it is so congested and shortened that it appears as a mere leafy cone at the top of the root. Like the girdle region of a horse-chestnut twig, it has come into existence by intense crowding of the nodes and shortening of the internodes. The question will arise as to how such a stem can avoid the shading of one leaf by another. This is prevented by the ingenious device of differen-

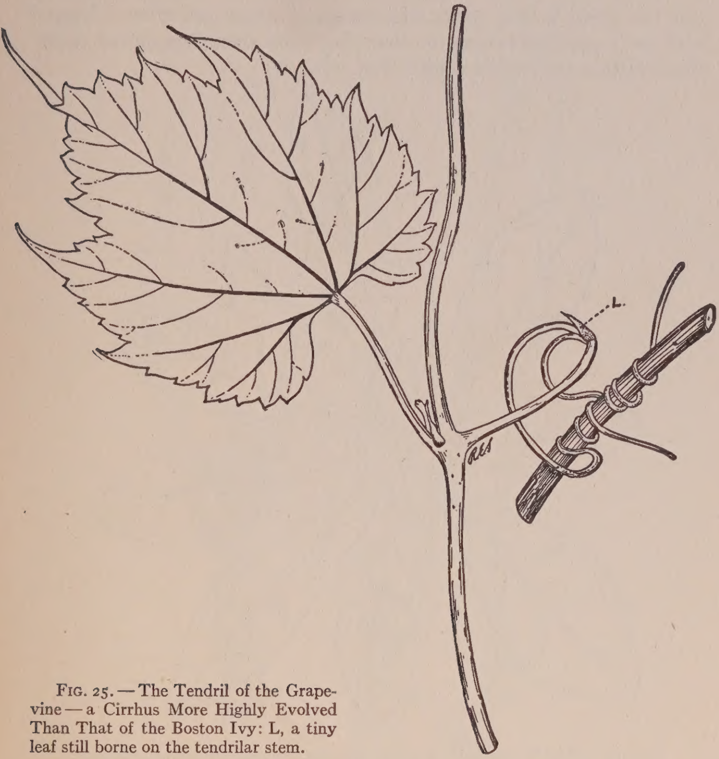

Fig. 25. — The Tendril of the Grapevine — a Cirrhus More Highly Evolved Than That of the Boston Ivy: L, a tiny leaf still borne on the tendrilar stem.

tial lengthening of the petioles. It is evident that a steep 2/5 spiral phyllotaxy may be shortened into a depressed spiral without interfering with the relative positions of the leaves, though No. 6 would of course lie almost directly over No. 1. But if the petiole of No. 1 be lengthened so that its blade falls outside the shadow of No. 6, then all will be well. This is actually what happens in "stemless" plants, and the result is the *rosette*, the leaves of which are often adjusted with such exquisite symmetry that they rival the arrangement of the pieces in an actual radial mosaic (Fig. 26).

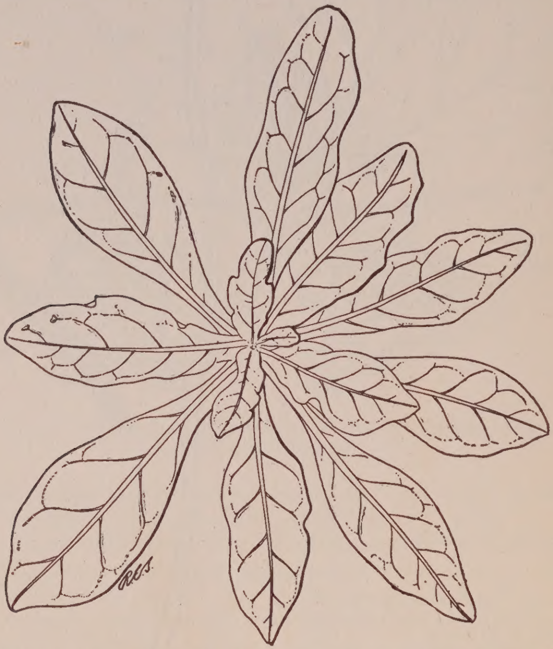

Fig. 26. — The Winter Rosette of the Evening Primrose (*Œenothera biennis*).

Many common plants pass the winter in the rosette state. It is a means of protection against browsing animals and against extremes of temperature and dryness. The growth of the stem upward as new leaves develop is prevented by active contraction and shortening of the root. This is often so intense that the outer bark near the crown is folded and corrugated, since the outer parts will not contract as will the inner.

f. The short-shoot or brachyblast. One of the most interesting organs for displaying leaves to best advantage is the short-shoot, dwarf branch, or brachyblast. It is found in certain of our cone-bearing trees — notably in the pines and larches — and is also characteristic of that peculiar tree, the ginkgo or maidenhair, which is known to be a close relative of the pine.

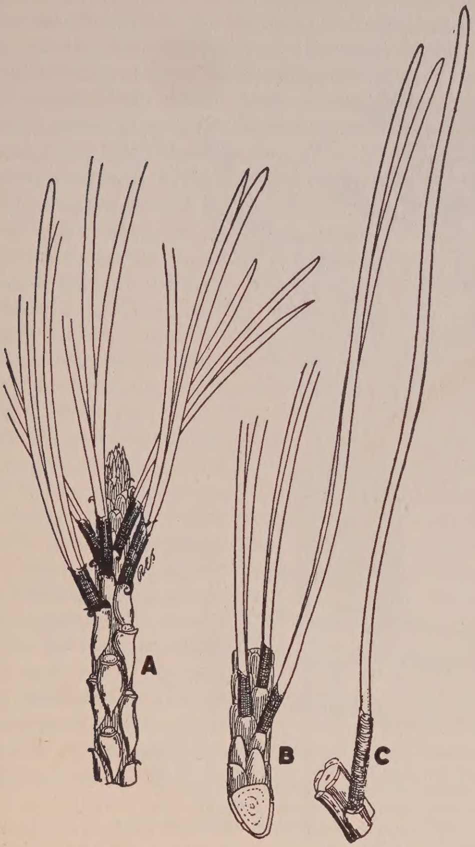

FIG. 27. — A, magnified drawing of the twig of yellow pine (*Pinus rigida*) with three-foliate short-shoots borne in the axils of decurrent scales. On the lower part the scales and short-shoots have fallen; B, similar drawing of the two-needle pine (*Pinus resinosa*); C, drawing of single short-shoot of *Pinus monophylla*.

The evolution of the brachyblast will serve as another excellent illustration of orthogenesis. Suppose we first examine the organ as it occurs on pine-trees. As is well known, pines bear their needles in bundles of two to five, and these are densely clustered over the branches (Fig. 27, A, B). Few people realize that these bundles are actually small lateral shoots which produce their few needles and then cease to grow any more. Such dwarf branches are technically called *brachyblasts*. Close examination shows that they stand in the axils of small brown scales which are proved to be extremely reduced leaves, since on young pines and on traumatic shoots they develop into long green needles (Fig. 29). The scales are continued downward (*decurrent*) along the twig, forming what are called *leaf-cushions*.

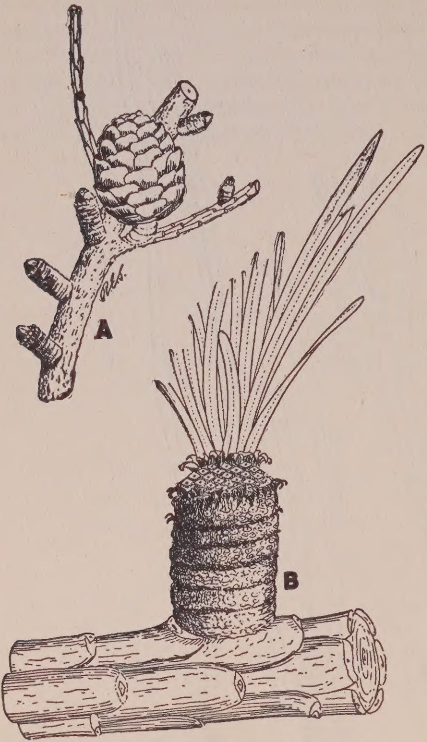

FIG. 28. — Short-shoots (Brachyblasts) of the Larch (*Larix europea*): A, habit sketch of a branch in the winter state bearing several short-shoots and a cone; B, single brachyblast in summer condition, enlarged to show annual growth increments and scars left by fall of needles and bud scales.

If we study the brachyblast in some detail, we shall find that it consists of a tiny core of wood surrounded by bark; it is closely sheathed with imbricated scales at the base and carries its few needles at the tip. Unlike most branches it bears no terminal bud. It remains on the tree about two years and then falls away completely.

The larch, a close relative of the pine, has a much larger and more sturdy brachyblast which persists year after year and produces each year a new set of leaves, though it never grows in thickness (Fig. 28).

Hence a cross-section through a brachyblast of any age exhibits but one ring of wood. But the larch-tree, along with its sturdy and persistent brachyblasts, shows certain other highly significant features. If we examine the long shoots in the summer, we shall find that they bear, not brown scale-leaves like the pine, but well-formed green needles. In the autumn these needles turn yellow and drop away, leaving a plating of leaf scars and leaf-cushions on the twigs. The following spring some of the buds which stood in their axils push out into brachyblasts. Not all the buds develop, however; in fact they are completely aborted in most of the leaf axils. This is an interesting correlation with the large size and multifoliate character of the short-shoots. If the latter grew out from every leaf axil, the branch would be congested with short-shoots beyond all reason.

Let us note with what admirable precision the pine works out its allied but more difficult problem. The leaves on its long shoots are scale-like and contain no chlorophyll. Hence if the pine is to have any green foliage at all on its new branches, it is forced (unlike the larch) *to develop its short-shoots the first season.* Moreover, these shoots bear but a few needles apiece, and to provide sufficient green foliage for the physiological needs of the tree they arise from every leaf axil. In consequence the pine with numerous few-leaved brachyblasts attains the same end as the larch with its fewer but multifoliate brachyblasts.

The short-shoot character is not confined to the conifers. Certain advanced seed plants (e.g. *Cercidophyllum*, *Psedera*) have adopted it, as has also the remarkable ginkgo tree. The latter is one of the most ancient of living trees. It was once widespread through the Americas, Europe, and Asia and had many relatives. To-day its race has completely disappeared except for the one species, *Ginkgo biloba*, which grows wild in the mountains of China. The Chinese and Japanese reverence it as a sacred tree, and it has been grown for centuries in their temple gardens. It takes kindly to America, which was once its native home, and is widely planted as a decorative tree. The ginkgo is closely related to the pine, and the short-shoots are homologous, although those of the ginkgo are large and sturdy like those of the larch.

Let us now ask the question: Do the pines possess the short-shoot in its primitive condition, and did it progressively evolve into the much larger short-shoot of the larch and of the ginkgo; or did the reverse take place, and is the pine condition one of reduction from a more highly differentiated state (regressive evolution)?

Evidence for either hypothesis may be sought along the lines of reversion, recapitulation, and paleobotany. The new short-shoots which arise on wounded branches of pines may produce strong terminal buds, but such never occur on normal ones. According to the theory of traumatic reversions, this is a recall of a previous normal condition and it suggests that at one time the pine short-shoot continued to grow year after year just as those of larch and ginkgo do. Furthermore, on such traumatic branches the axillating scale beneath the short-shoot reverts to a chlorophyll-bearing needle (Fig. 29). All this implies that the brachyblast of the modern pine, as well as its axillating scale, has been reduced from a former more highly differentiated condition.

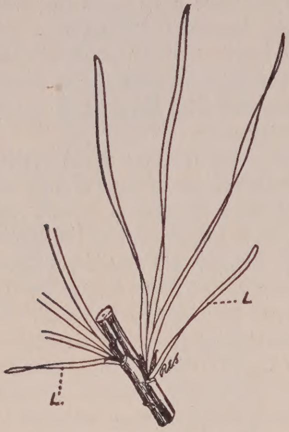

Fig. 29. — Part of a Twig of Yellow Pine (*Pinus rigida*) Which Grew Out from a Stump after the Tree Was Felled. The twig bears two short-shoots; the axillating leaves, which are normally brown scales, have reverted to long green needles (L).

The evidence derived from recapitulation is also cogent. Young pine seedlings bear long green needles in place of scale-leaves.

The matter has been conclusively settled by a striking discovery which was made in paleobotany some years ago. On Staten Island there are deposits of Cretaceous clays. While digging these for brickmaking some years back, the workmen came across considerable deposits of plant debris — twigs, wood, pine-needles, cones, seeds, bark, etc. This find was called to the attention of scientists, and finally several hundred pounds of the clay were taken to Professor Jeffrey's laboratory for close study. After treatment with alkali and softening reagents, much of the material became amenable to microscopic investigation. As a result of the studies a flood of light was thrown upon the history of several plant groups and notably upon that of the pines. Much of the material turned out to be the debris from ancient pine-trees, and among the fragments were numerous well-preserved short-shoots with their needles. All these exhibited strange and archaic features, and all possessed growing terminal buds. Most curious of all, however, was the short-shoot of a tree which has been called *Prepinus*.* As the name suggests, it is believed to be an actual ancestor of the pine. The short-shoot of *Prepinus* was a bulky structure comparable to that of *Ginkgo* and bore about twenty needles (Fig. 30). Furthermore, it possessed a great terminal bud and must have continued its

* E. C. Jeffrey, "On the Structure of the Leaf in Cretaceous Pines." *Annals of Botany*, XXII (1908).

growth year after year. Such a feature, as we have said, is quite different from that of normal short-shoots of modern pines.

To-day, then, without fear of contradiction, we can say that *Prepinus* has settled the short-shoot question and has shown us that the modern pine condition is a reduced and degenerate state of an organ much more highly developed in the pines of the Cretaceous Period. To make the matter even more striking, it may be added that in the Western United States lives a pine (*Pinus monophylla*) whose short-shoots bear but one needle (Fig. 27, C). It seems to represent the terminal member of the orthogenetic series beyond which no advance is possible.

Let us then recapitulate the general subject of brachyblast evolution in its historical sequence:

1. One of the most ancient of pine-trees — *Prepinus* of the Cretaceous Period — bore its twenty or more leaves on heavy short-shoots which possessed strong apical growth.

2. *Ginkgo biloba*, the sole survivor of an ancient race closely allied to the pines, still has a short-shoot very similar to that of *Prepinus*. The larch, a member of the *Pinaceæ*, seems to have retained the archaic condition.

3. Other Cretaceous pines had reduced the needles to three, four, or five, but still possessed rudimentary buds on their brachyblasts.

4. Modern pines rarely have more than five needles, and have completely lost the terminal bud. Traumatic stimuli (reversion phenomena) may bring it back and also restore the subtending scale to the form of a green leaf. Seedling pines, too, are covered with green needles instead of scales.

5. *Pinus monophylla* bear but one needle on its short-shoots and completes the regressive orthogenetic series.

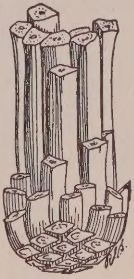

FIG. 30. — The Brachyblast of *Prepinus statenensis*, an Extinct Pine of the Cretaceous Period. The needles have all been broken off.

In this discussion we have tried once more to show the value of historical studies of living things. The modern world is what it is because of what it has been. Into our bodies, into the bodies of all plants and animals, are integrated millions of years of evolution. Our customs, our laws, our ceremonials, our architectural and ornamental designs, our very beliefs, are likewise the evolutionary result of thousands of years of human thinking and experiment. The singular vitality of the "dead past" is astonishing. In order to get a unified view of any thing, it is necessary to study more than the present aspect. For we suspect that the real being of any object is in a higher dimensional world, though to human thought it exists in past, present, and future. Hence we get at least one step closer to a complete understanding when we study its past as well as its present state.

B. ADAPTATIONS TO THE STORAGE OF FOOD AND WATER

As one of their general functions, all stems have the function of storage. A few tree-trunks store so much starch that it may become of economic importance. From the pith of the sago-palm (*Metroxylon Rumphii*) the starch may be washed out and granulated into pearl-like masses, one tree yielding from 400 to 600 pounds of sago.

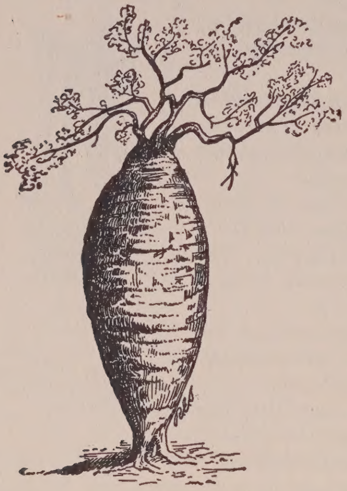

FIG. 31. — The Bottle-tree (*Cavanillesia tuberculata*) of Brazil. (Adapted from Kerner.)

When the ability to store food and water becomes particularly developed, the result is an inflated and swollen stem. In the dry regions of Brazil grows a certain cotton-tree (*Cavanillesia tuberculata*) whose stem is swollen out like a barrel (Fig. 31). As a miniature copy of the cotton-tree may be mentioned the kohl-rabi, which is grown as a stem vegetable.

If we suppose such a swollen stem to retreat under the soil, the result is a *corm*. A corm is a globose and swollen stem, and not a root as is commonly supposed. Its true morphology is evidenced by the fact that it bears brown sheathing leaves in whose axils stand small buds. Both the crocus and the gladiolus are cormose plants. The corm should not be confused with the bulb; the latter is a large subterranean leaf bud borne on a very short stem.

C. MODIFICATIONS OF THE CREEPING AXIS FOR REPRODUCTION AND STORAGE

Just as the upright axis may be modified for food and water storage, so may the creeping axis; but in addition, such axes usually serve for reproduction. An interesting series may be traced from stolon to tuber, and undoubtedly the various stages illustrate the progressive specialization through which the tuber was evolved.

Stolons are lateral branches which creep outward a short distance from their parent plant and take root at the tip. The leaves on their creeping part are usually reduced, but a strong terminal bud is present. Eventually the connection with the mother plant dies away and thus many young daughter plants become isolated around the parent. These may in their turn become stoloniferous. The stolon is a very efficacious reproductive organ, and many weeds are largely reproduced in this way. One need only mention the orange hawkweed (*Hieracium aurantiacum*, Fig. 32), and the Indian tobaccos (*Antennaria sps.*).

If such lateral creeping branches become very elongate and slender, they are called *runners*. Rooting at their tips, they send up new plants which in their turn push out new runners. In this way chains of a dozen or more plants may be produced. The strawberry is a well-known plant with the runner habit. New strawberry plants are grown almost exclusively from small plants produced in this way.

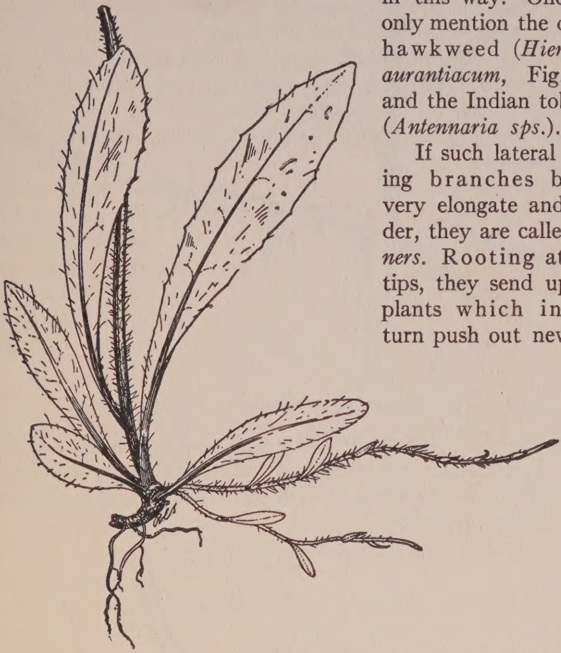

FIG. 32. — The Orange Hawkweed (*Hieracium aurantiacum*), a Stolon-bearing Plant.

Stolons and runners are reproductive devices. When, however, the stolon or runner retreats under the soil, it is called a *rhizome* and usually adds the function of storage to that of reproduction. All stages occur between the stolon, which lies on the surface, and the subterranean rhizome. Sometimes the branch may begin life as a stolon and later plunge into the earth as a rhizome. Superficially the stolon and the rhizome differ in color, the former being green and the latter white. In place of the green leaves of the stolon, the rhizome bears colorless scales. It is clear, however, that these scales are only reduced leaves, for they bear buds in their axils and these often become lateral axillary branches.

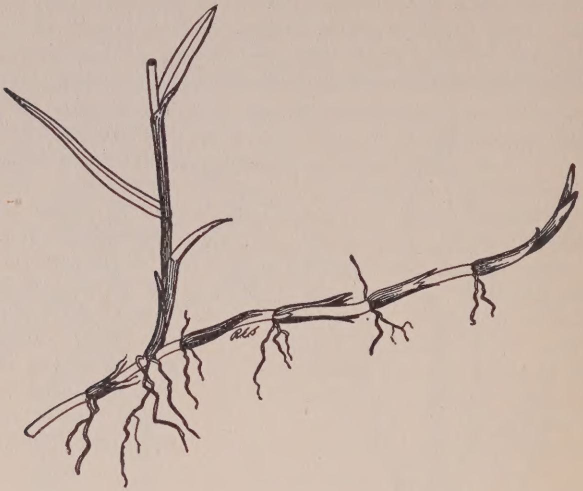

FIG. 33. — Rhizome of the Witch-grass (*Agropyron repens*).

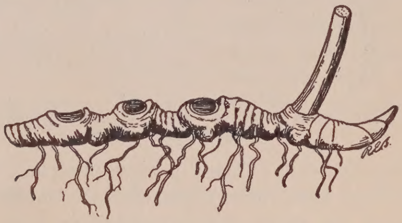

FIG. 34. — Rhizome of Solomon's Seal (*Polygonatum biflorum.*)

The witch-grass (*Agropyron repens*, Fig. 33), a most pernicious weed on cultivated soils, has a remarkably developed rhizome system which takes root at every joint as it creeps along. Its tips often turn up into the air and produce new green plants. It is evident that such a plant revels under attacks of the hoe and cultivator, since it is thereby broken up and distributed. The fragments are very tenacious of life. Grasses and sedges are often rhizomatous, and the interlacing of these organs is hardly inferior to systems of ramifying roots in preventing the wash of soils and the drifting of coastal sands.

Many of our early-flowering woodland plants are rhizomatous. One may recall the Solomon's seal (Fig. 34), wild oats, bloodroot, wild ginger, etc. Such modifications are closely correlated with the habits of these plants. During the growing season they store food actively in the underground stem; then in spring they push through the dead forest litter and in a few weeks are in full flower and fruit. Thus they carry out their most essential life processes before the green canopy of the trees above them shuts off the light. By mid-July, having stored up a supply of food for the next season's use, they turn yellow and lie dormant till the next spring. Such plants comprise an ecological group known as *tropophytes* (Greek *trope* = "a turning"), since they have the power to turn or adjust themselves to varying environmental conditions. Other tropophytes characterize desert regions where a little rain falls at a certain time in the year only. Their underground storage roots, corms, rhizomes, or bulbs enable them to lie dormant many months waiting for the rain. When this does arrive, they spring magically into life and the "desert blossoms like the rose."

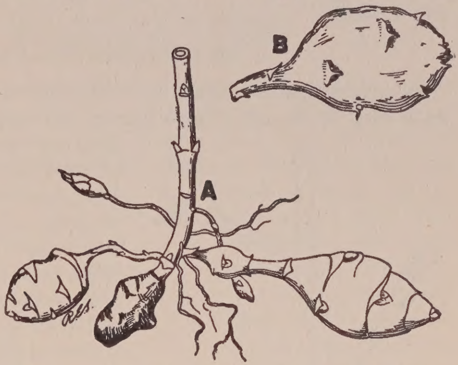

FIG. 35. — A, cluster of tubers of the artichoke (*Helianthus tuberosus*); B, young tuber of the potato with scale-leaves and axillary buds.

In one of Wells's tales called "The First Men in the Moon," a striking flight of the scientific imagination pictures the reawakening of what we would call most extreme tropophytes after the long and rigorous lunar night.

At the terminus of the rhizome series, and as a specially devised storage organ, stands the tuber, familiar to us all in the common potato. The potato is the swollen distal extremity of a rhizome, and its true morphology becomes clear enough when we realize that the "eyes" are clusters of buds, and that even the subtending leaf itself is present as a tiny triangular scale beneath each eye (Fig. 35, B).

Less metamorphosed than the potato are the tubers of the artichoke — *Helianthus tuberosus* (Fig. 35, A).

So we reach the end of another of Nature's long lines of progressive experimentation — the line in which she transformed creeping stems into rhizomes and tubers. We can summarize the steps by saying that branches, which were originally upright, took on the creeping habit and became transformed into short stolons for reproduction. Elongating still more, they became the efficient organs called runners. Entering the earth, they lost their chlorophyll, reduced their leaves to scales, assumed the new function of storage, and became rhizomes. Finally the rhizome became congested with food and was transformed into a tuber.

D. MODIFICATIONS FOR DEFENSE

Many familiar plants are beset with thorns and prickles. If we ask what may be the use of such organs, the answer will usually be that they are weapons of defense to ward off browsing animals. When we realize, however, that thorns are particularly characteristic of plants which grow in hot, dry regions, we begin to wonder if the thorny character does not really have its explanation in a direct stimulus which is exerted by the environment. This seems to be partially substantiated by experiments, for if some thorny plants are grown in a moist atmosphere, they tend to lose the spiny character.

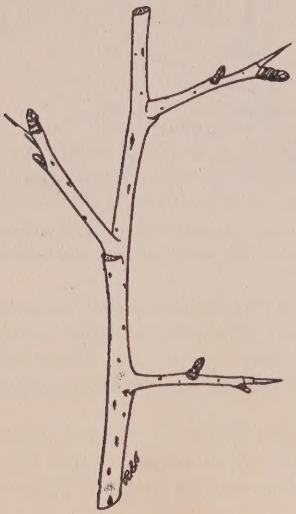

FIG. 36. — Thorny Branch of the Plum.

Whatever may be the final explanation of thorns they can be traced through a gradually perfecting series just as can short-shoots or rhizomes. As an introduction to the series, let us consider the plum and note the organ from which Nature evolved one kind of thorn. On many varieties of plums it is not uncommon to find the stems beset with tapering, rigid, sharp branches which are well covered with leaves in summer and with buds in winter (Fig. 36); they are often an annoying nuisance when one is pruning such trees. Such sharpened twigs represent the thorn in its incipiency, and like any other branch they grow from axillary buds and bear leaves. A step in advance is taken by the hawthorn bushes. We find them covered with cruelly sharp daggers (Fig. 37), but it is easy to see that these, too, stand just above the leaf scars and that their smooth sides bear tiny marks whence scales must have fallen; they are also beset with lenticels, which is of course another normal stem feature. If we observe young growing hawthorn branches in spring, we will discover that shoots are developing from the axils of many of the leaves and that they themselves bear small green scales (Fig. 38). But they quickly cease their growth, taper to a point, lose their reduced leaves, harden, and become the sharp thorns so characteristic of the plant. There can be no question but that they are lateral branches.

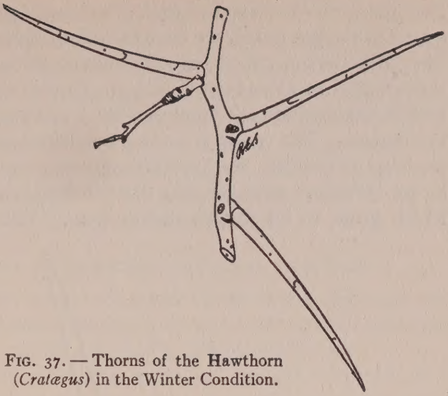

Fig. 37. — Thorns of the Hawthorn (*Cratægus*) in the Winter Condition.

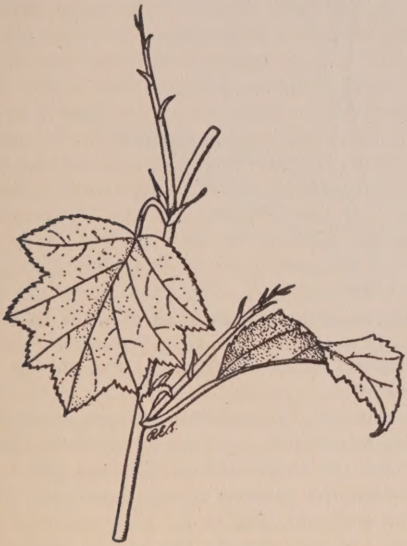

Fig. 38. — Branch of Hawthorn in Spring. The thorns arise in the leaf axils and bear tiny scale-leaves.

Allied to the rose family, to which the plum and the hawthorn belong, is the pea family. Many of its members, too, have remarkably developed thorns. In the dryer parts of Africa they produce dense thorn thickets which are almost impassible. Among native plants of the pea family we have the honey locust (*Gleditsia trichanthos*), the old trunks of which become covered with branched thorns sometimes a foot or more long (Fig. 39). In this case not only is the main axis of a lateral branch involved, but a group of secondary axes enters the system. The result is a ferocious compound weapon with points as sharp as needles. In Argentina grows a close relative of the honey locust (*Gleditsia amorphoides*) the trunk of which bristles with thorns which grow to be sixteen inches long. This tree forms dangerous thorn woods in which cattle are sometimes injured. The natives call the tree *espina de corona Cristi.*

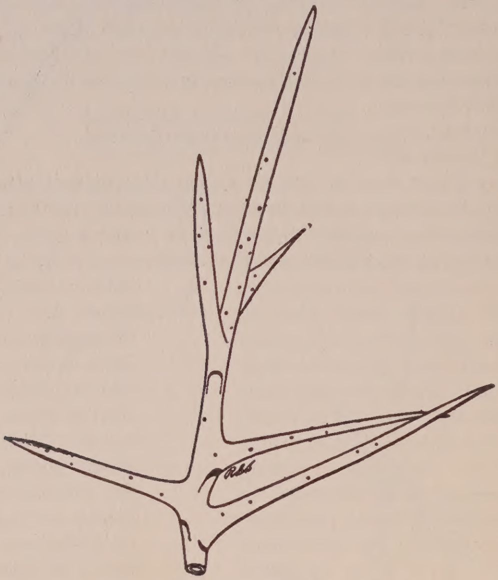

FIG. 39. — Single Branching Thorn of the Honey Locust (*Gleditsia trichanthos*).

A very curious phenomenon may be mentioned here in connection with the thorns of *Acacia sphærocephala*, an African leguminous shrub. They are inflated at the base and in the hollow inflations, which are called *myrmecophilous domatia*, live colonies of very fierce ants which defend their homes as the medieval knights did their castles. "So soon as this standing army of ants detects the foe, it commences offensive operations, like the garrison of a fortress, and by biting and squirting formic acid frighten the invader away." Thus the tree is kept free of leaf-eating enemies, borers, etc. Strangely enough it seems to reward the kind protection of its guests, for it produces from the edges of its leaves pellets of nitrogenous matter — the so-called Belt's bodies — which are eagerly gathered by the ants. This looks like a case of symbiosis between a plant and an insect. By *symbiosis* we mean an association of two organisms for mutual benefit. In the case under discussion the ants receive food and protection, while the plant is kept free from insects which might be harmful to it.

E. MODIFICATIONS TO SUBSERVE THE LEAF FUNCTION

All young stems have a layer of green tissue in the bark and are consequently able to manufacture food, though later as cork develops this green tissue may be cut off and shed in the form of scales.

In some cases plants undergo a great reduction in the size and number of their leaves, and this may lead to such an extreme state that the stem is obliged to take over the leaf function. Under these conditions it often becomes flattened like a leaf and comes to simulate one so closely that careful study is necessary to detect the mimicry. In fact, whenever chlorophyll becomes abundant in an organ that organ tends to assume the flattened form. This is, of course, an advantage, for it permits light to penetrate to all parts just as it does in a leaf.

In the manner now familiar to us of studying such a series, let us start with a stem very little modified from its original state. Such a one is that of the broom plant, *Cytisus scoparius*. It is a native of Europe but sometimes escapes from cultivation in America. In habit it consists of a brush of long, slender, green twigs which bear but few leaves. Plants with this habit are rather common in dry desert areas and are called "switch plants."

More advanced than the broom is the common garden asparagus. All are familiar with the appearance of its stout stems as they push through the soil in spring. Their leaves are reduced to white or purplish scales. Later in the season the stout simple stems grow into much-branched systems beset, not with green leaves, but with a mist of tiny green branches, but even as on the vernal stems the leaves themselves are reduced to scarious, axillating scales.

The broom and the asparagus have shown no flattening of the stems, but in the tapeworm plant (*Muhlenbeckia platyclada*) the branching green axes are flattened like jointed ribbons, though they still produce a few weak leaves at the nodes (Fig. 40, A). Such stems are logically called *phylloclades* (Greek *phullon* = "leaf" + *clados* = "branch").

In considering the adaptation of the stem to the leaf function we are bound to think also of certain cacti. These plants, natives of the dry regions of North America, have lost almost all trace of leaves, and as a result the stem has had to come forward and modify itself to do the work which would ordinarily devolve upon the leaf. Most extreme are the *Phyllocacti*, whose flattened, jointed stems are a familiar sight in conservatories. Most cacti, in addition to using their

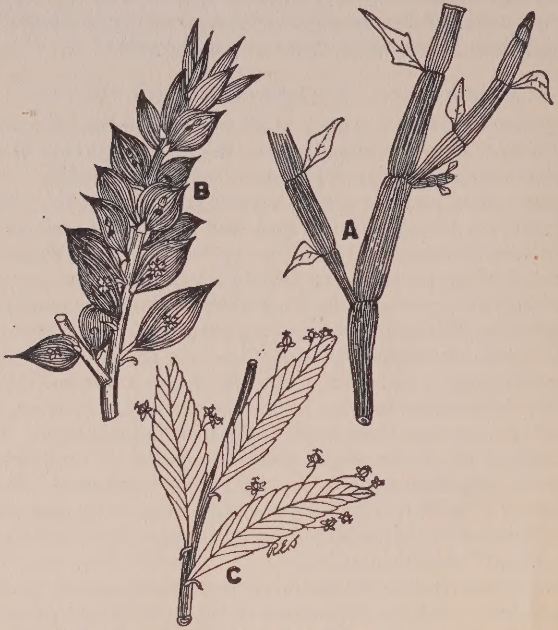

FIG. 40. — Phylloclades and Cladophylls: A, phylloclade of the tapeworm plant (*Muhlenbeckia platyclada*); B, cladophyll-bearing branch of the butcher's broom (*Ruscus aculeatus*); C, cladophylls of *Phyllanthus speciosus.*

stems for food-making, also use them for the storage of food and water. The swollen, inflated, fleshy forms of the *Cerioideæ* are clearly adapted to this purpose. But not all cacti are without leaves; the lemon vine or Barbadoes gooseberry (*Pereskia aculeata*) is a climbing cactus with large, fleshy, green leaves. The seedlings of many common cacti bear awl-shaped leaves, and the young growth is also liberally provided with them. Such leaves soon dry up and fall away so that the fleshy adult plants are leafless. Cactus spines are probably much modified branch systems which rise from the leaf axils.

We have said that cacti are natives of North America. They take kindly to dry habitats over the earth and are so well established along the Mediterranean coast and in Asia Minor that they appear like a regular part of the native vegetation. In fact, painters have been guilty of introducing them into Biblical scenes.

Moving still higher in the series of forms, we find that flattened stems not only mimic leaves in their green and expanded features but may actually begin to simulate leaves in shape also. Such organs are borne by *Ruscus*, the butcher's broom, a plant which is dried, dyed red, and much used to-day in Christmas decorations. Its branches are seemingly covered with harsh, sharp-pointed leaves (Fig. 40, B). If, however, the plant is observed when in bloom, it will be found that clusters of tiny bracted flowers are growing out from the flat faces of the "leaves." Of course the true explanation of this seeming paradox is that the heart-shaped organs are not leaves but stems. Further study reveals the fact that they themselves rise from the axils of small scale-like leaves. Botanists apply the term *cladophylls* (the same two word-roots as in *phylloclades*, but in reverse order) to branches which closely mimic leaves in color and shape. *Phyllanthus*, illustrated in Fig. 40, C, is another plant which bears cladophylls; the position of the small flowers is enough to give the secret away.

Florists also grow an African vine which passes in the trade as "smilax," though it is really a member of the genus *Myrsiphyllum*. Just as in *Ruscus* it seems at first sight to be covered with heart-shaped shining leaves. But these organs arise from the axils of white scales, and although they never produce flowers as does *Ruscus*, yet their anatomy as well as their position proves that they are cladophylls.

It will now be evident why a physiological definition of an organ as "the tool of a function" might lead to many misunderstandings. According to such a definition the leaf is the organ whose chief function is to make starch, yet here is a stem which is every bit as efficient in starch-making as any leaf. Physiologically it is a leaf: morphologically it is without doubt a stem. To pull away the disguises from such highly specialized organs and to trace their evolution from basic types is the business of comparative morphology.

CHAPTER V

THE LEAF

26. *Phylogeny of the Leaf*

According to the theory of Lignier which we have been following, the leaf was derived from the lateral branch system of an ancient thallus plant. The fern bears a leaf which is probably of a more ancient type than that of the seed plant, and there is evidence that fern leaves were derived from a primitive dichotomous foliar organ. The leaves of certain ancient ferns (*Botryopterideæ*) were constructed much like stems with sets of radiating twig-like branches which forked again and again till they ended in flat blades. This surely suggests that leaf and stem were originally the same thing — members of a richly branched thallus whose axis became a stem, perhaps of sympodial derivation — and whose side members became leaves (Fig. 8).

27. *Ontogeny of the Leaf*

Leaves originate ontogenetically from the growing point as small elevations which slowly increase in length. They grow rapidly on their abaxial surface and consequently come to curve inward upon one another and thereby protect the soft and delicate growing point. Gradually they differentiate into a blade and petiole, and then by rapid growth on the adaxial surface they straighten out and expose their blades to the light.

The green leaf is the great food-making organ of the plant, and its typical form is an expression of the fact; it is like a sheet of chlorophyll spread out to intercept light. It receives salts from the soil and gases from the air, and in its laboratories called cells it synthesizes starch and other foods. Since it is essentially the light-receiving organ, its form and position are governed by the direction of the light.

28. *Functions of the Leaf*

A. LIGHT ADAPTATIONS

(1) *Leaf Mosaics.*

We have had occasion already to speak of leaf mosaics when considering stemless or acaulescent plants. Perfect mosaics, however, are found also on upright plants and are particularly well developed when the foliage is thick, since a leaf is of small use if it is shaded and concealed. Go into a woodland where the tree canopy is not too dense and observe the arrangement of the shrubs and herbs which cover the forest floor. The leaves are adjusted with great nicety, for by twisting and differential elongation of petioles and by fitting small leaves between large ones every inch of available area is taken and each leaf receives the maximum illumination. It has been thought, too, that the much dissected leaves so characteristic of certain plants are also adaptations to permit the unimpeded flow of light downward through the plant. Mosaics are particularly well developed on plants which climb over walls and other supports. In such cases the illumination is unilateral and the mosaics are expressions of the fact, since each blade is held perpendicularly to the incident light.

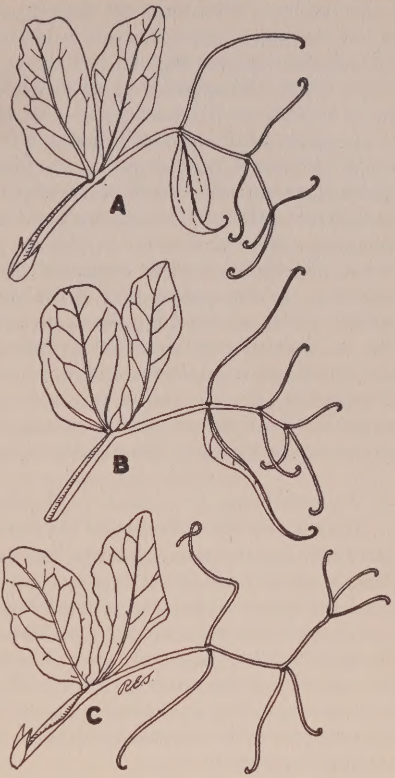

FIG. 41. — Drawings of Three Leaves Gathered from a Row of Sweet-peas (*Lathyrus odoratus*): A, six leaflets have been converted into tendrils, and a seventh is barely starting to transform; B, here the transformation of a similar leaflet has proceeded much further, and the green tissue of the blade is almost lacking; C, transformation wholly accomplished with the persistent midrib functioning as a tendril.

It has been pointed out by botanists that plants which form dense stands, such as grasses, sedges, and cat-tails, incline to have narrow leaves which are held almost vertically. Because of this habit, though each leaf receives little light, yet in the aggregate more light is received than would be possible otherwise.

In forests where the dense canopy of tree-tops permits almost no rays of white light to filter through, floor vegetation is practically lacking and only such colorless plants as toadstools and uncanny Indian-pipes or coral-roots can develop. It is said, too, that the floor of the tropical forest is likewise a place almost barren of plant life. "Far above the trees expand their crowns, and all lesser plants madly climb, twine, and scramble to reach the light, there to throw out their leaves and flowers in a mad riot of color and perfume."

To assist weak stems in bringing about the best light relation the leaves sometimes become partly modified into climbing organs. A type leaf, as we realize, consists of a blade traversed by veins, a petiole, and stipules. All these parts in one plant or another have been modified to serve as climbing organs. In *Gloriosa*, a beautiful climbing lily, the tips of the blades become elongated into tendrils and wind around supports. In the sweet-pea it is the ribs of several of the terminal leaflets which are used for the same purpose; for proof of this, see Fig. 41. In the native clematis or virgin's-bower (*Clematis virginiana*), and also the plant grown in our flower-beds under the name nasturtium (*Tropæolum*), the leaf petiole is sensitive to contact and coils around supports. To complete the type examples, in the cat-briers and the carrion-flower (*Smilax*), the stipules become delicate tendrils.

(2) *Protection from Too Intense Light, Heat, and Evaporation.*

Thus far we have considered the leaf as adapted to maximum illumination. In some cases, however, the maximum is too much. Perhaps the intense light and heat vibrations tend to produce something in the plant analogous to sunburn; perhaps they provoke too great evaporation of water and there is danger of death from desiccation. However this may be, many plants are modified to withstand intense insolation. By means of waxy coats, thick epidermis, hairy coverings, sunken water-pores, rolling of the leaf and rosette formation they can resist the austere conditions of their habitats. Such extreme dry-land plants are called *xerophytes*.

An interesting modification of leaf position related to the subject under discussion is found in the "compass-plants." We can do no better than to quote Kerner's description of them. "Healthy living plants as they grow in the sunny meadow look as though they had been laid between two gigantic sheets of paper, somewhat pressed, and dried for some time in the way plants are prepared for herbariums, and had then been removed from the press and set up so that the apex and profile of the vertical leaf blades point north and south, i. e., in the meridian; while their surfaces face east and west. This inclination is so well and regularly observed by the living plants on the prairies, that hunters are enabled to guide themselves over such regions, even under a clouded sky, by means of these plants." The advantage of this position is that the sunbeams in the heat of midday can only strike the leaves obliquely, but in the coolness and dampness of the early morning and late afternoon the light may strike them at right angles. That this interpretation is correct is attested by the fact that the same plants when growing in shaded and moist places do not exhibit the compass character.

The phenomenon of leaf-fall is also intimately related to excessive water evaporation. In speaking of the branch in its winter condition we noted the many protective devices instituted to reduce evaporation. We pointed out, further, that the fall of the leaf, as a rhythmical phenomenon of our temperate forest, must have been instituted during the oncoming of the Glacial Period. We must admit that we do not know just how such a feature could be impressed on a plant, though some recent work suggests that the whole thing is more closely related to decrease of light in the autumn than to lowering temperature.

There are certain other movements known as *nyctotropic* or *sleep movements* which the leaves of plants exhibit when light begins to grow dim. The two lateral leaflets of the clover-plant fold their under surfaces together at night, while the terminal leaflet droops over the other two. The meaning of such movements is obscure.

B. ADAPTATIONS TO THE WATER LIFE

At the other extreme from the xerophyte, which is adapted to dry soils, there are plants which live wholly in the water and are logically called *hydrophytes*. The more intimate study of these ecological groups of plants is deferred to a later chapter, but at this point we may note that the aquatic life influences the leaf profoundly. Such leaves are of two general types; those which float on the water, and those which live wholly submersed; the former have air pores or stomata only on the upper surface, they are often waxy-coated, and, as everybody must have observed, water runs off them as it would off a duck's back, so that the air pores do not become clogged. Submersed leaves, on the contrary, are usually very delicate; their veins are so poorly developed that they cannot support themselves in the air; they have no waxy cuticle, and so they dry up in a few minutes when removed from the water. In certain extreme cases the whole plant body may be so profoundly modified for the water life that it comes to mimic an alga or a lichen (duckweeds and podostemads).

C. ADAPTATIONS TO FOOD AND WATER ABSORPTION

We almost hesitate to speak of this phenomenon since so many students get the wholly false impression that plants absorb water through their leaves. This is not true for the great majority of plants. The root is the organ given over to the function of water absorption. Still, all of us have noted that badly wilted plants will revive when sprinkled with water and placed in a dark and moist atmosphere. This does not mean that water has passed in through the leaves; it means that water evaporation from the leaves has been temporarily checked, since evaporation into an atmosphere saturated with water vapor does not go on, and this has made it possible for the leaves to receive a supply of water from their stems or roots and hold it, thereby restoring their flaccid tissues to firmness. Furthermore, the pores of the leaf close in darkness and this naturally makes possible the retention of water.

A few plants, however, do depend almost wholly on their leaves for their supply of water and salts. Particularly notable in this connection are certain members of the pineapple family (*Bromeliaceæ*), whose leaves are sometimes grown together at their bases to form reservoirs in which water accumulates along with humus debris. This decoction is absorbed by odd shield-shaped hairs borne on the leaves. Sometimes the reservoirs become the homes of an aquatic plant (*Utricularia*) which may send out stolons from one fountain to another and cover its home with festoons. Mez, a German botanist, kept a bromeliad suspended free from roots and in good health for a year by filling its fountains with water containing the necessary inorganic salts.

Well known to all of us is another member of the pineapple family — the Spanish moss (*Tillandsia usneoides*). This queer plant hangs in gray beard-like streamers from trees along watercourses all through our Southern States. In its adult condition its root has completely dried up into a small, clinging, horsehair-like strand fastened around the branch, and consequently the plant must get its water and its salts through its scaly leaves. *Tillandsia* is rather shy on flowers and seeds, but fragments of it are drifted by the wind and it is well liked by birds for building nests, which proceed to grow as if nothing had happened to the plant. In the moist tropics *Tillandsia* may become a nuisance by loading down telephone wires.

D. LEAVES ADAPTED TO STORING FOOD AND WATER

(1) *Agaves and Aloes.*

Here again we may study a series of forms gradually approaching perfection. Many plants utilize their leaves for storing water and food; this is particularly true of desert plants, among which the agaves and the aloes are conspicuous. The former are wonderfully developed on the dry table-lands of Mexico, and more than 325 species have been described from Mexico and the West Indies. They are often called century-plants, since popular opinion has it that they flower only once in a hundred years. This, however, is not true; many flower at a much earlier age, though some have never been found in flower at all. During their extended vegetative life they store up quantities of food and water in the leaves, then in one supreme effort they transfer all this material into a giant flower cluster and perfect their seed. This often so weakens the plant that its leaves fall limply on the ground and it dies, depending on its seeds to carry on the race. Plants like this, which flower and fruit but once in their life and then pass away, are called *monocarpic.*

For another and similar modification, but one which is a bit of an improvement over the agave condition, the common cabbage will serve. In this plant the thick leaves become filled with food and water and closely wrapped together to form a bud. The cabbage is a biennial, and the reserves stored in one year are utilized in the second for seed production.

(2) *The Bulb.*

If we suppose such a leaf bud to retreat beneath the soil, the result is a form of storage organ very common among plants and called a bulb. The bulb may also be considered as a modified rosette plant whose leaves have become swollen with food and closely imbricated upon one another. There are two types of bulbs — the scaly, and the coated or tunicated. An example of the former is the lily bulb (Fig. 42, B, C), in which the numerous thick scales are lance-shaped and imbricated. The onion bulb, on the other hand, is tunicated (Fig. 42, A). Its scales completely enwrap one another, forming concentric coats, so that in cross-section such a bulb presents the appearance of numbers of rings, one within another.

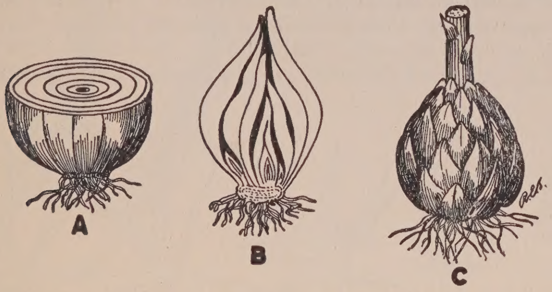

FIG. 42. — A, tunicated bulb of onion cut in cross-section; B, longisection of tunicated bulb of tulip showing terminal and axillary buds; C, scaly bulb of lily.

E. LEAVES ADAPTED TO SERVE AS THORNS

We have seen that a tendril may be morphologically either a stem (grape, passion-flower, squash) or a leaf-part (clematis or pea). In like manner, thorns and prickles are not always stems, but in some cases are obviously derived from leaves. One of the most striking cases is the three-pronged thorn of the barberry. Its position as an axillating organ is sufficient to establish its morphology (Fig. 43), but this is not all the evidence, for on strongly developed suckers or on shoots which arise after severe pruning one may sometimes find all transitions from the normal leaf to the triradiate or even uniradiate spine (Fig. 44).

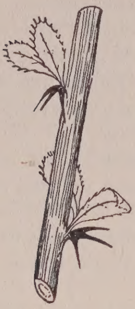

Fig. 43. — Barberry Twig with Leaf-prickles as Axillating Organs.

F. LEAVES ADAPTED TO REPRODUCTION

Not rarely leaves are found that are able to assist in the asexual reproduction of the plant. The walking-fern (*Camptosorus rhizophyllus*) has a long, narrow, triangular blade running out to a caudate tip which often takes root, and from adventitious buds new plants develop which in their turn may form new walking-leaves. As a result, three or four plants may come to be attached one to another in a manner analogous to the way young strawberry plants are held together by runners (Fig. 45). Certain other ferns are also able to produce buds on their leaves which may develop into small leafy plants before they fall away and assume an independent life. Several greenhouse plants are commonly propagated by leaf-cuttings; such are the begonia and gloxinia. If fragments of the leaves be stuck into moist sand or even pegged down flat, they develop adventitious buds and roots along their edges wherever a vein comes to the margin. Most striking of all, per-

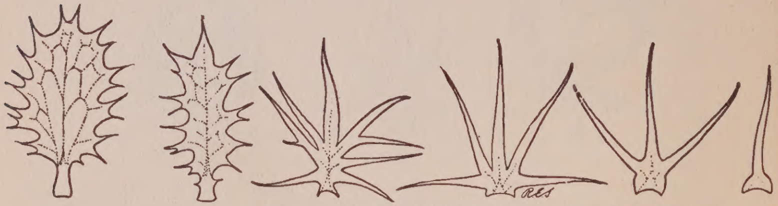

Fig. 44. — Barberry Prickles: a series taken from base to apex of a single rapidly growing sucker showing the gradual transformation from leaf to uniradiate prickle.

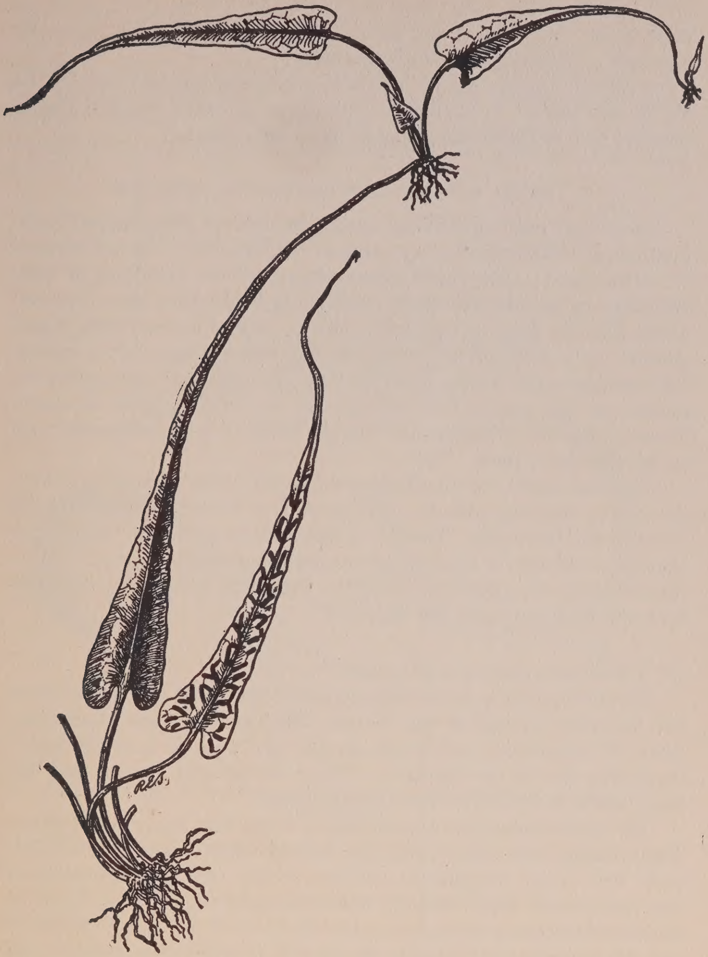

FIG. 45. — The Walking-fern (*Camptosorus rhizophyllus*), a Fern Whose Leaves Take Root at Their Tips and Produce New Plants.

haps, is the life-plant (*Bryophyllum*), whose leaves, even when attached to the parent plant, often send out little plants from every notch on their sides. Any leaf of this plant when laid on moist soil sends up numbers of plantlets in a similar manner.

A certain begonia has the power to produce small plants all over its leaves and stems. It is really a hybrid but is called *Begonia phyllomaniaca* — a rather striking species name for a plant.

G. LEAVES ADAPTED TO CARNIVOROUS NUTRITION

Under this heading we have to consider some of the strangest modifications of leaves which are known to the botanist — leaves adapted to eating meat. They have always attracted the attention of both botanists and non-botanists, and many weird tales have been invented about gigantic flesh-eating plants with enormous leaves which might swallow up a man. When we learn that nothing larger than beetles and centipedes are ever captured by even the largest of the carnivorous plants, we can realize that such stories are wholly flights of fancy. These plants are queer enough in truth without there being any need to tell lies about them.

There are said to be about 500 species which supplement their nitrogen diet by trapping animals. In general they have devised three ways of capturing their prey. The first group catches it in a sac from which there is no escape; in a second group the leaves perform certain movements and finally close over the prey; while in a third group the prey is caught on sticky hairs and digested.

(1) *The Bladderworts or Utricularias.**

The bladderworts are mostly aquatic plants, and already we have had occasion to speak of one of them which grows in the water-fountains of bromeliads and feeds on the tiny aquatic animals which commonly live in the fountains. There are several species that are fairly common in the ponds in New England.

The bladderworts are rootless plants which float freely in the water. Their leaves look like repeatedly forked threads and are thickly beset with small, transparent bladders which vary between two and five millimeters in diameter in different species (Fig. 46). Each of these bladders has a circular mouth of which the lower rim is thickened and the upper lateral borders of which bear long, branched hairs or antennæ. From the dorsal part of the mouth hangs down a valve or flap of which the free margin fits into a mucilage-containing groove in the lower rim. Hence the opening into the sac is sealed by a water-tight valve. On the lower part of the valve stand four stiff, sharp hairs which point outward (three only are shown in our figure); they are related to a kind of contractile or motor tissue in the valve itself, and may be called trigger-hairs, since their function is to explode the whole device. The long antennæ which rise from the upper corners of the mouth spread out into a sort of funnel but are not irritable. The whole interior is lined with four-armed hairs which absorb the liquids in the bladder.

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* See C. L. Withycombe, "On the Function of the Bladders in *Utricularia vulgaris*," *Journ. Linn. Soc. Bot.*, XLVI, 401–413 (1924).

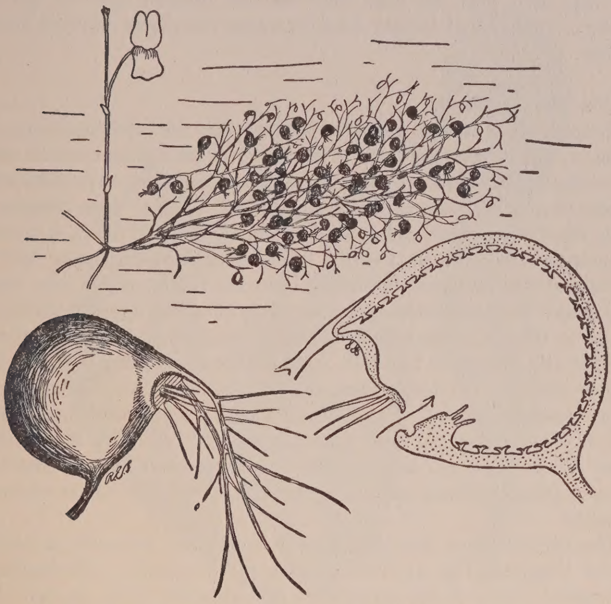

FIG. 46. — Plant of *Utricularia* with External and Sectional Views of a Single Bladder-trap.

Let us now see how this curious device functions. Since the hairs inside the trap constantly absorb water, and since the valve is water-tight, a negative pressure is set up and the walls of the bladder are crowded slightly inward. If a water animal inadvertently touches any one of the four trigger-hairs on the valve there is a sharp response — the valve instantly draws up, a current of water rushes into the bladder, and the unfortunate creature is swept to its death. For the valve is a one-way door and like the portal of Hades might well be inscribed: "All hope abandon, ye who enter here." The animal soon suffocates or starves, and there is evidence that its remains are actually digested by enzymes analogous to those in our own gastric juice. In about thirty minutes to an hour the small trap is set for another catch.

The prey consists of small crustacea, insect larvæ, worms, and the like. Sometimes young fish are trapped, and in one instance a tadpole was seen with its head held by one bladder and its tail by another. Remains of twenty-four crustacea have been counted in one bladder.

(2) *The Pitcher-plants.*

Entirely unrelated to the bladderworts are the pitcher-plants, the blades of which have the form of a pitcher or cup often covered over with a flap or lid. They are smooth and glassy inside and are beset with thousands of stiff, downward-pointing hairs. Each of these cisterns is partly filled with water, and around the rim is secreted a film of honey; furthermore the lower part of the leaf is green but the upper part is veined and marbled with crimson. Thus the whole device may seem to an insect like some brilliantly colored flower. But suppose an insect to land on the rim to feed on the honey; it may naturally creep beyond the edge and, losing its foothold, fall into the cistern beneath. Swimming to the wall, it tries to climb out, but is met by the thousands of sharp, needle-like hairs. It falls back into the water and finally dies from drowning; then the body putrifies and the brownish, fetid water of the cup is absorbed into the plant. It has been proved that the leaves of pitcher-plants secrete digestive enzymes just as do our own stomachs.

The pitcher-plant just described is *Sarracenia purpurea,* a native of New England (Fig. 47, B). Another pitcher-plant — *Darlingtonia californica* — lives in the mountains of California (Fig. 47, A). Its leaves are hooded at the top and from the slit-like mouth beneath projects a flattened and forked part of the blade which suggests a fish's tail. The whole leaf curiously resembles a hooded snake with the tongue thrust out. The hood is beautifully veined with purple and between the veins the leaf tissue is so thin that light can penetrate, so that from the inside there would seem to be a skylight in the roof. As in *Sarracenia,* honey is secreted around the mouth, but woe to the insect which stops to eat, for it slips into the cistern beneath. Now most of the insects which *Darlingtonia* catches are winged forms, which of course try to fly out by directing themselves toward the skylight, but they are only knocked back again and again till they are finally drowned; never do they find the opening by which they entered.

It is said that the *Darlingtonia* pitchers are sometimes filled with eight to ten centimeters of decaying animal remains. After digestion is accomplished the pitchers contain only claws, mandibles, wing covers and other chitinous pieces.

Another strange thing about this business where all things are strange is that a small fly (*Sarcophaga Sarraceniæ*) lays its eggs in the decaying mass of insect remains, where the larvæ grow to maturity and then bore through the pitcher wall to pupate in the earth. The adult fly has learned to pass in and out of the pitchers without harm. The question may be asked: Why aren't the grubs also digested by the plant? The same question may be raised concerning the parasites which live in our own intestines; perhaps their thick cuticle protects them; perhaps they secrete anti-enzymes which neutralize the action of the digestive juices.

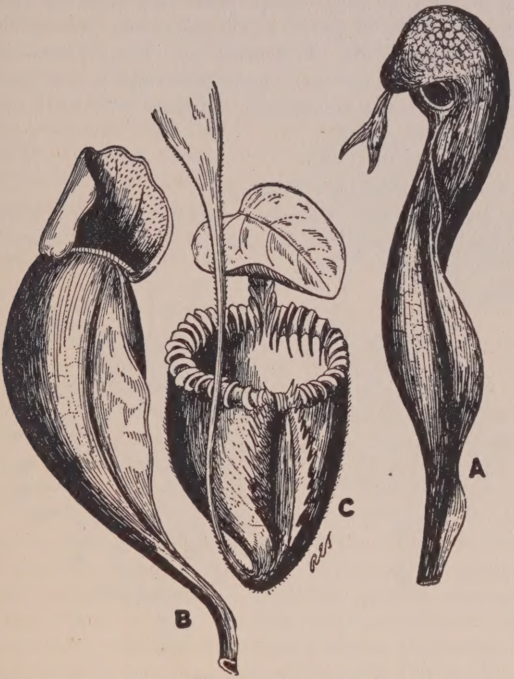

FIG. 47. — Leaves of Three Species of Carnivorous Pitcher-plants: A, *Darlingtonia californica;* B, *Sarracenia purpurea;* C, *Nepenthes sp.*

One more genus of pitcher-plants must be mentioned; these are the *Nepenthes* species, natives of the hot Indo-Malayan region, and are sometimes grown in conservatories (Fig. 47, C). Their pitchers are slung at the end of long, climbing petioles and are often brilliant with color. *Nepenthes Rajah* has a pitcher large enough to accommodate a pigeon, though this does not mean that pigeons are ever caught in them. The trap is very effective, since around the mouth is a circle of large, sharp, downward-pointing spines "like the teeth of a beast of prey" which effectively prevent the escape of unlucky insects. The *Nepenthes*, too, often have "nepenthes worms" living in their pitchers. Some years ago a species of amœba new to science (*Amœba nepenthesi*) was discovered in the pitcher of one of these plants.

(3) *The Sundew and Venus's Fly-trap.*

Thus far we have described arrangements of chambers in which animals are trapped. In the sundews and Venus's fly-trap, however, other ingenious mechanisms have been contrived for catching prey.

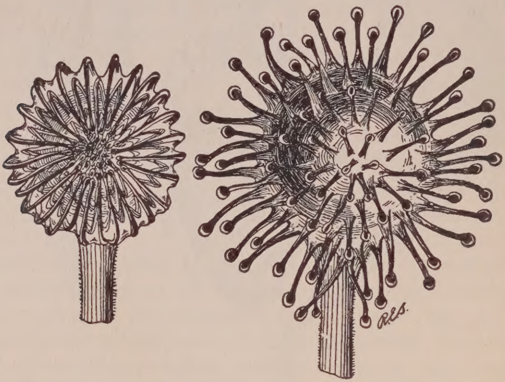

FIG. 48. — Leaves of the Round-leaved Sundew (*Drosera rotundifolia*) in the Open and Closed Condition (x4).

The sundews, of which we have two rather common species (*Drosera rotundifolia* and *Drosera longifolia*), are also swamp plants. The leaves of *D. rotundifolia* (Fig. 48) are some four to five centimeters long and are borne in the form of a rosette, each being shaped like a spatula or spoon with a flat circular bowl. The bowl part — really the leaf blade — is covered with radiating red hairs all lying in the plane of the leaf when the trap is set. Each hair secretes at its tip a glistening drop of sticky fluid.

Suppose now a small insect, say a mosquito, attracted by the glistening "dew," alights on the leaf. It becomes entangled in the viscid liquid even as it would on sticky fly-paper. As soon as the stimulus is felt, the hairs begin to bend inward somewhat as the fingers of the hand may flex into the palm; the movement occupies about ten minutes, during which the tips of the tentacles converge upon the insect and pour an acid digestive juice upon it. After two or three days all the soft parts of the prey are absorbed. Then the tentacles straighten out again and the dry residue is blown away. The trap secretes new liquid and is ready for another catch.

Most remarkable of all the groups of moving traps is that of the Venus's fly-trap (*Dionæa muscipula*) which grows on our Atlantic coastal plain from Long Island to Florida (Fig. 49). This is a rosette plant like *Drosera*, but the petiole of the leaf is broadly winged and the spoon part or blade is hinged down the middle. The margin is beset with long, stiff spines, while on each half of the blade are three shorter spines. If the surface of the blade be touched, the two halves fold together in a manner resembling the closing of a partly opened book, while the marginal spines interlock just as one's fingers do when the two hands are folded together. Suppose a small insect alighting on the leaf has been the exciting cause; it is trapped before it is aware, crushed flat, and digested by a copious flow of juices. The whole movement of closing takes only about ten to twenty seconds.

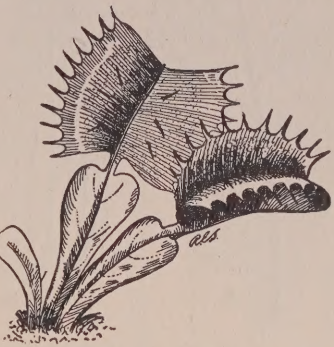

FIG. 49. — Two Leaves of the Venus's Fly-trap (*Dionæa muscipula*).

(4) *The* Fly-catcher (*Drosophyllum lusitanicum*).

The fly-catcher will serve as an example of those carnivorous plants which catch their prey by means of sticky hairs much in the same manner as does the sundew, but without movement of the hairs. It is a plant which grows in dry rocky soils in Portugal and Morocco. Its grass-like leaves are beset with beads of sticky secretion in which insects become entangled and subsequently digested. It is said that the peasants hang the plant up in rooms to get rid of flies.

29. *Leaf Terminology*

In describing plants the botanist makes considerable use of the leaf characters such as the shape, nature of base, apex, margin, etc. The set of technical terms which apply to such characters is rather large and formidable, for botany is an old science and in the progress of the centuries it has picked up an elaborate terminology. Many of the terms, however, are rarely seen to-day. In the following treatment we have included only those in common use among botanists and horticulturists. One cannot properly describe plants till such a set of terms is mastered.

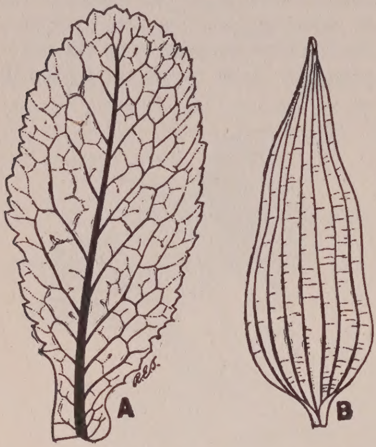

Fig. 50. — The Two Fundamental Types of Leaf Venation: A, leaf of turnip with net or reticulate venation; B, leaf of a monocot with parallel venation.

A. VENATION

There are two fundamental types of leaf venation (Fig. 50). If the ultimate minute veinlets form a complicated network between the major veins then the leaf possesses net or *reticulate venation*. On the contrary, if the veins are rather numerous, run parallel to one another, and are connected by minute straight veinlets, the leaf is *parallel-veined*. Net-veined leaves are much better adapted to resist the tearing effect of winds than are parallel-veined leaves, since their veins are usually tied together along the margin. A parallel-veined leaf like that shown in Fig. 51 is easily whipped in pieces by the wind. A banana leaf is somewhat like this and a banana plantation after a wind storm is a place of shreds and tatters.

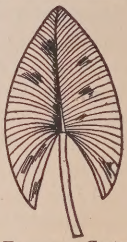

Fig. 51. — Costal Parallel Venation.

Net-venation may be either *pinnate* or *palmate*. In the former the lateral veins spring from the sides of a strong midrib (Fig. 50, A). The venation is said to be palmate, on the contrary, when the veins radiate from the apex of the petiole like the fingers of a hand (Fig. 55, B). Parallel-veined leaves which possess a strong midrib and many lateral veins (Fig. 51) are called *costal-veined* (*costa* = "a rib"), while those like Fig. 50, B, are *basal-veined.*

It has always been a problem to botanists to account for the two types of leaves having such different venation. Net-veined leaves characterize the dicotyledons, while parallel-veined leaves are borne by most monocotyledons. Many years ago De Candolle put forward what is called the "phyllode theory." In essence this theory is that the parallel-veined leaves of the monocotyledons are not homologous with the net-veined blades of the dicotyledons but are flattened petioles in which the leaf-traces naturally run parallel to one another.

There is considerable evidence for this view. First of all the flattening of a leaf petiole to simulate a blade occurs in several families of dicotyledons; it is well seen, for example, in certain acacias (Fig. 53). Hence the transformation which De Candolle's theory contemplates certainly can occur. Yet these acacias may still bear net-veined compound blades at the tip of their flattened and green petioles. The blade of the monocotyledons, however, is usually parallel-veined and actually seems to be a new development — the flattened end of the petiole itself. There is some proof of this too. Common in rivers and ponds are certain plants known as water-weeds of the genus *Potamogeton.* The leaves of some of them are of two kinds; those which grow beneath the water are ribbon-like and seem to be mere flattened petioles. Those which float on the water, on the contrary, have flattened, oval, parallel-veined blades. And all transitions between the two forms can be found, from mere slight broadening of the apex of the ribbon leaf to the full parallel-veined blade (Fig. 52).

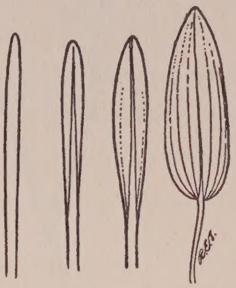

FIG. 52. — Transition from Submerged Linear Phyllode to Floating Leaf with Ovate Blade in a River Weed (*Potamogeton*).

The whole subject can be nicely interpreted by the law of the irreversibility of evolution. Suppose that for some reason, orthogenetic or other, the blade of the dicotyledon became progressively reduced till it was finally lost. Then the petiole had to assume the phyllode condition. If the need for a true blade ever rose again, the blade would have to be manufactured from the tip of the phyllode, and consequently it would not be homologous with the net-veined blade of the dicotyledon, but instead would correspond to part of the petiole of the latter. Mrs. Arber, an English worker, has recently been

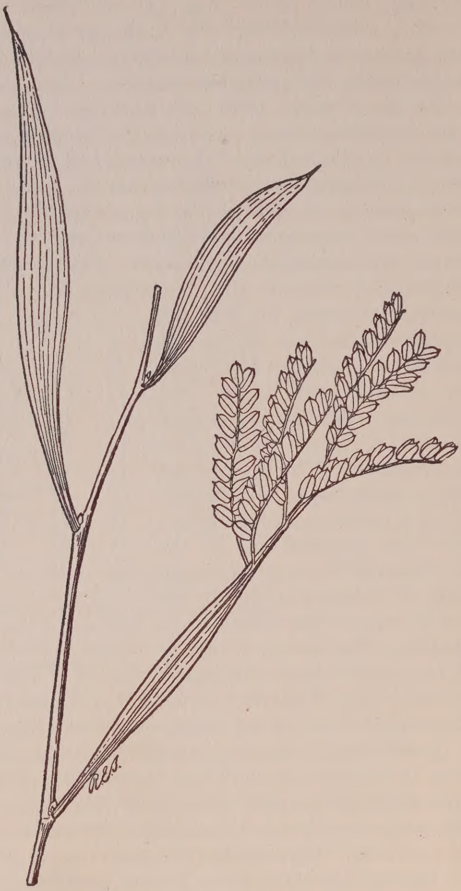

FIG. 53.— Twig of *Acacia Koa*, var. *hawaiiensis*. The petiole of the lowest leaf is flattened out into a phyllode, but it still bears a compound blade. The two upper leaves are reduced to phyllodia only.

accumulating anatomical evidence for the truth of the phyllode theory of monocot leaves.

B. LEAF SHAPES

We come now to the shapes of leaf blades. The major idealized types are given in Fig. 54. It should be noted that the narrow strap-shaped leaf can be considered the primitive type. By broadening below the middle there arise lanceolate, ovate, and deltoid shapes. By broadening in the middle there arise elliptical, oval, and even orbicular and reniform shapes; while oblanceolate, obovate, cuneate, and spatulate leaves are the result of broadening above the middle.

CLASSIFICATION OF LEAF SHAPES

A. *Linear* (*linea* = "a line"): shaped like a strap and several times longer than wide.

BROADEST BELOW THE MIDDLE

B. *Lanceolate:* shaped like a lance-head, several times longer than broad, widened just above the base and tapering to the apex.

C. As in Fig. 54, C. (The term *lanceolate* is sometimes applied to this form also.)

D. *Ovate* (*ovum* = "an egg"): like the section of a hen's egg with the broad end down; a very common shape.

E. *Deltoid:* a modified ovate leaf with straight sides and consequently shaped like the Greek letter delta.

BROADENED NEITHER ABOVE NOR BELOW

F. *Oblong:* about twice or three times as long as broad and with parallel sides.

G. *Elliptical:* in the shape of a narrow ellipse several times longer than broad.

H. *Oval:* a much broader ellipse, approaching a circle.

I. *Orbicular* or *rotund:* circular.

BROADEST ABOVE THE MIDDLE

J. *Oblanceolate:* a lanceolate leaf such as B, inverted.

K. *Obovate:* the ovate leaf like D, inverted.

L. *Cuneate* (*cuneus* = "wedge"): the deltoid leaf like E, inverted.

M. *Spatulate:* spoon-shaped, with a rounded upper part and a "handle."

C. LEAF BASES

The following terms apply not only to bases but also give names to more or less ovate leaves with such bases (Fig. 55).

A. *Cordate* (*cor* = "heart"): leaf base turned in to form a sharp notch; hence, possessing the conventional form of a heart.

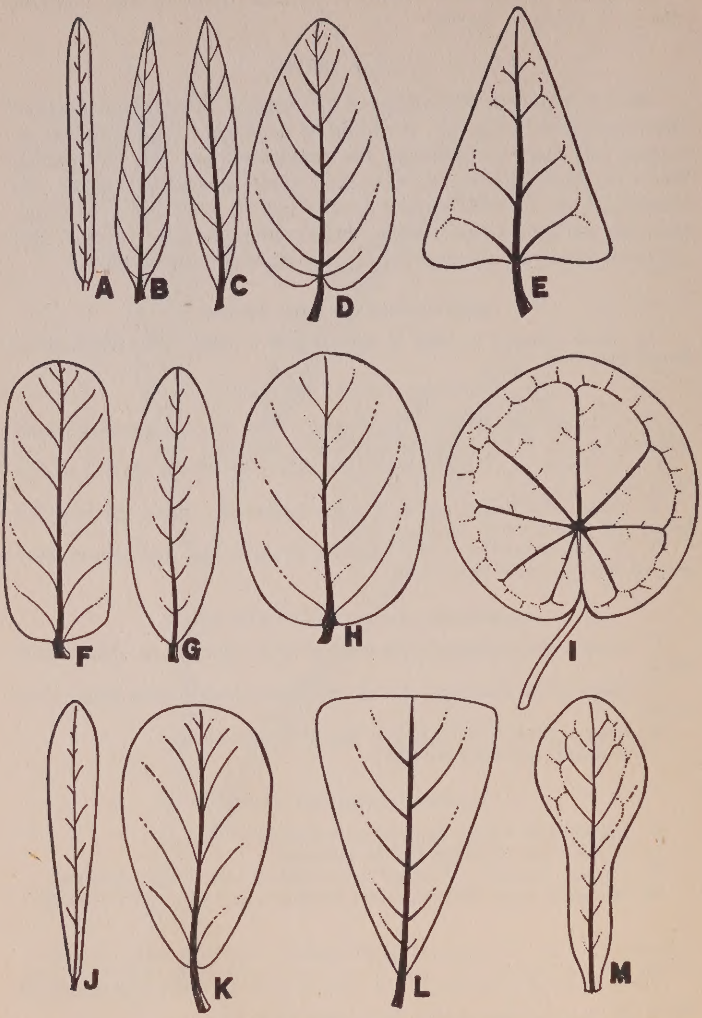

FIG. 54.— Leaf Shapes: A, linear; B and C, lanceolate; D, ovate; E, deltoid; F, oblong; G, elliptical; H, oval; I, orbicular; J, oblanceolate; K, obovate; L, cuneate; M, spatulate.

B. *Reniform* (*ren* = "kidney"): shaped like the longisection of a kidney; whole leaf broader than long.

C. *Auriculate* (*auricula* = "little ear"): basal lobes prolonged into blunt "ears."

D. *Hastate* (*hasta* = "spear"): basal lobes sharp, prolonged backward and flaring away from the petiole.

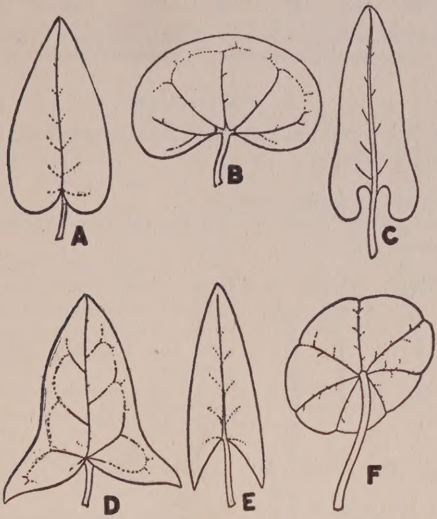

FIG. 55. — Leaf Bases: A, cordate; B, reniform; C, auriculate; D, hastate; E, sagittate; F, peltate.

E. *Sagittate* (*sagitta* = "arrow"): basal lobes sharp, prolonged backward parallel to the petiole.

F. *Peltate* (*pelta* = "shield"): a leaf with petiole attached to the lower surface of the blade producing the effect of a shield held out on an arm.

D. LEAF EXTREMITIES

Several of these terms can also be applied to leaf bases (Fig. 56).

A. *Acuminate:* tapering to the apex; if the tip is long and tail-like, the term *caudate* is used.
B. *Acute:* ending sharply without tapering.
C. *Obtuse:* ending with a blunt tip.
D. *Truncate:* as if suddenly cut off transversely.
E. *Retuse:* possessed of a very shallow reëntrant notch.
F. *Emarginate:* reëntrant angle a decided notch.
G. *Obcordate:* with a heart-shaped notch.
H. *Cuspidate* (*cuspis* = "point"): tipped with a sharp point like a tooth.
I. *Mucronate:* tipped with a bristle like a continuation of the midrib.

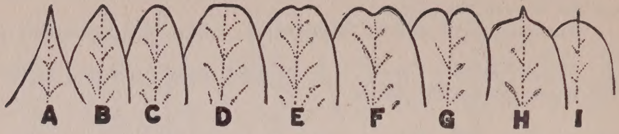

FIG. 56. — Leaf Extremities: A, acuminate; B, acute; C, obtuse; D, truncate; E, retuse; F, emarginate; G, obcordate; H, cuspidate; I, mucronate.

E. LEAF MARGINS

The following terms are applied to leaf margins; the cuttings in all cases are shallow (Fig. 57).

A. *Entire:* wholly without cutting.

B. *Serrate* (*serra* = "a saw"): with fine saliencies directed forward like the teeth of a saw.

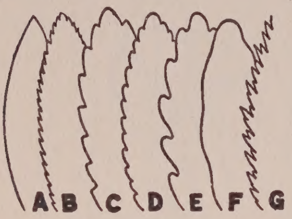

FIG. 57. — Leaf Margins: A, entire; B, serrate; C, dentate; D, crenate; E, sinuate; F, repand or undulate; G, incised.

C. *Dentate* (*dens* = "a tooth"): with larger teeth which commonly project outward rather than forward.

D. *Crenate* (*crena* = "a notch"): with the marginal teeth blunt and rounded.

E. *Sinuate* (*sinuare* = "to wind or bend"): with the margin a strong sinuous line.

F. *Repand* (*repandus* = "bent backward"): with the margin but slightly waved.

G. *Incised* (*in* + *cædere* = "to cut"): with the margin slashed irregularly with sharp cuttings none of which reach half-way to the midrib.

F. LOBATION AND SEGMENTATION

If the marginal cutting penetrates more deeply, the leaf becomes *lobed* or *segmented*. The following forms are distinguished:

A. *Lobed:* when the division does not extend more than half-way inward and either the sinuses or lobes are rounded.

B. *Cleft:* with the divisions extending half-way or more to the midrib and with sharp sinuses.

C. *Parted:* with divisions reaching almost to the base or to the midrib.

D. *Divided:* with divisions reaching quite to the base or midrib and converting the simple blade into a compound leaf.

G. COMPOUND LEAVES

The divisions of the compound leaf are called *leaflets*. Depending on their origin, compound leaves may be either *palmate* or *pinnate*.

The number of leaflets present can be indicated by such terms as *multifoliolate*, *trifoliolate*, etc. Some leaves are several times compounded, and terms such as *bipinnate*, *tripinnate*, etc., are used to describe them. When the leaf is two to several times palmately or pinnately compound, the term *decompound* may be used.

A compound leaf can be distinguished from a leafy branch by the fact that in autumn the entire structure falls away from the stem; furthermore, there are no buds in the axils of leaflets as there are in leaf axils. Leaflets are usually jointed to their support and may fall separately from the rachis before the petiole itself is detached from the stem. From this fact it can be determined that certain leaves which appear simple and have but one blade are actually reductions from a previous multifoliolate condition. Such is the leaf of the barberry, whose single leaflet is jointed to the apex of the petiole; it is a unifoliolate compound leaf, paradoxical as the term may appear. Certain barberries (section *Mahonia*) have compound leaves of several leaflets, and this may be considered as the primitive condition for the whole genus.

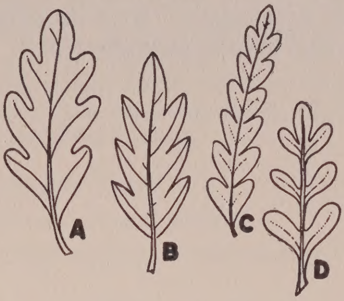

FIG. 58. — Lobation and Segmentation: A, pinnately lobed; B, pinnately cleft; C, pinnately parted; D, pinnately divided.

H. ATTACHMENT OF LEAVES TO STEMS

Most leaves are attached by a stalk or petiole to the stem axis and are consequently said to be *petiolate*. Some, however, dispense with the petiole and become *sessile*. When the sessile base more or less encircles the stem, the term *clasping* is employed. Sometimes two opposite sessile leaves are united at their base forming a shallow cup through the bottom of which the stem seems to pass. Such stems are *perfoliate* and the leaves are said to be *connate*.

I. LEAF OR STEM SURFACE FEATURES

The surface characters of leaves and stems are of considerable value in diagnosis of plants. The following terms are commonly employed. A *glabrous* leaf is smooth, with neither hairs or other removable material. A leaf provided with a dense coat of very fine hairs like fine pile on velvet is *pubescent*. When the hairs are longer but soft and individually distinct, the term *pilose* may be used. If the hairs are appressed and matted together but still straight, the leaf is *tomentose;* if on the other hand they are twisted and curled together, the term *wooly* is applied. Leaves beset with bristle-like hairs which are not particularly harsh to the touch are called *hispid,* while those decidedly harsh to the touch when stroked backward are called *scabrous.* Many leaves, stems, and even fruits are covered with a white, waxy "bloom" which often gives them a bluish cast. Such organs are said to be *glaucous.* When the material of the coat is a whitish dust or scurf the term *pulverulent* is used.

CHAPTER VI

THE INFLORESCENCE AND THE FLOWER

The term *inflorescence* is applied to the arrangement of flowers on an axis. It is a feature of considerable value in determining plants, since some families are characterized by certain types of inflorescence. Thus the parsley family (*Umbelliferæ*) receives its name from the fact that its inflorescence is umbellate, while the borage family (*Boraginaceæ*) is characterized by curious one-sided cymes.

30. *Inflorescence Types*

A. THE DETERMINATE INFLORESCENCE

There are two major types of inflorescence — *determinate* and *indeterminate.*

Suppose we consider that a forward-growing branch produces a flower at its tip; it is clear that this definitely determines and stops the growth of that particular axis. If any more flowers are to arise on that branch, they must spring from the axils of leaves (called *bracts* when associated with an inflorescence) lower down. Hence they arise on lateral or secondary axes. The forward growth of such lateral axes may be stopped by a terminal flower in a similar manner, and then tertiary axes may arise to carry on the flower production. Such a basal type of determinate inflorescence is called a *cyme.* From Fig. 59, A, it will be evident that the oldest flower (here represented by a circle) stands at the top of the main axis; or, if the inflorescence is spreading, it stands at the center of the flower cluster.

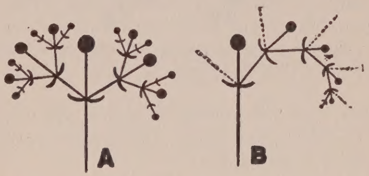

FIG. 59. — Determinate Inflorescences: A, the cyme; B, the one-sided or uniparous cyme.

One of the most characteristic modifications of the inflorescence just described is the *uniparous* or *one-sided* cyme. In this case but one lateral axis of a pair regularly develops, and when the whole structure straightens out it resembles that type of indeterminate inflorescence called the *raceme.* In Fig. 59, B, a dotted line shows the position of the hypothetical second axis.

B. THE INDETERMINATE INFLORESCENCE

The indeterminate inflorescence is much more common than the determinate and runs into many forms. In this type a terminal flower is never produced, and hence the main axis may theoretically continue to grow upward indefinitely, constantly producing new flowers. In actual fact it soon dwindles away and ceases to elongate. The flowers of this type of inflorescence are all produced on lateral axes (pedicels) of the second order and, of course, these axes like any other branches arise from the axils of leaves (bracts). In an indeterminate inflorescence the lowest or outermost flower is oldest.

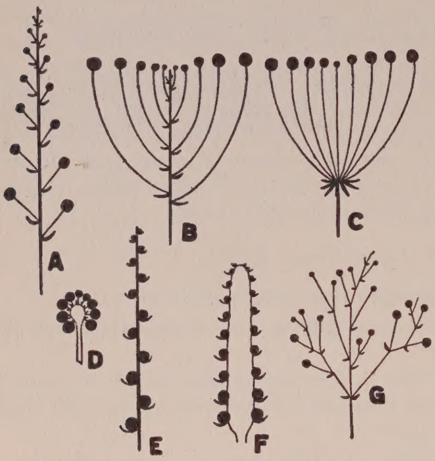

FIG. 60. — Indeterminate Inflorescences: A, raceme; B, corymb; C, umbel; D, head; E, spike; F, spadix; G, panicle.

The basal type of indeterminate inflorescence is the *raceme* (Fig. 60, A). Some of its modifications are the *corymb*, *umbel*, *head*, *spike*, *spadix*, *catkin*, and *panicle*. These may be defined as follows:

A. *Raceme:* an elongated flower axis with the individual flowers pedicellate and with the oldest ones at the bottom; hence the development of the inflorescence is *acropetal*.

B. *Corymb:* a modified raceme with differential elongation of pedicels to bring the flowers to a common plane.

C. *Umbel:* an inflorescence whose axis is suppressed and whose pedicels (called *rays*) spring from a common point and are about equal in length. The bracts of the pedicels are aggregated to form an *involucre*.

D. *Head* or *capitulum:* a kind of globose umbel with the pedicels very short or suppressed entirely.

E. *Spike:* like the raceme but without pedicels to the flowers. When the spike is drooping and flexuous, as in birches or willows, it is called a *catkin* or *ament*.

F. *Spadix:* a spike with a fleshy axis; characteristic of the arum family, where it is commonly associated with a brightly colored bract called a *spathe* (e. g.. Jack-in-the-pulpit or the calla "lily").

G. *Panicle:* a kind of irregularly compounded raceme.

Almost any inflorescence may become compounded; in this way arise compound racemes, umbels, etc.

THE FLOWER

31. *Introductory*

Arrived at the subject of the flower, we may begin to feel ourselves completing the circle of our studies on the plant, since the study of the flower naturally leads to the study of the fruit and seed. It was for the production of seed that the whole elaborate mechanism of the flower was evolved. With the flower are bound up some of the most interesting problems of botany, such for example, as the origin of flowers, the relation of flowers to insects, the evolution of flowers, and their bewildering variations. As Huxley says: "Flowers are the primers of the morphologist; those who run may read in them uniformity of type amidst endless diversity, singleness of plan with complex multiplicity of detail. As a musician might say: every natural group of flowering plants is a sort of visible fugue wandering about a central theme which is never forsaken, however it may momentarily cease to be apparent."

Botany, as we have remarked, is still to the layman the "study of flowers." The reason for this prevalent opinion is not far to seek. The biological sciences in the nineteenth century were largely devoted to the work of classifying plants and animals. As far as the higher plants go, the flower is the part which is most conservative and best shows their relationships. Hence, nearly all systems of classification are based on floral structure, and a vast literature and an extensive terminology has been accumulated concerning flowers and their modifications. This kind of botany was once the hobby of many amateurs and loomed large in the public mind, which has failed to follow the modern advances into the more abstruse fields of plant anatomy and physiology. Hence botany is still to many "the study of flowers."

32. *The Flower of the* Marsh-marigold (*Caltha palustris*), *Crowfoot Family* (*Ranunculaceæ*)

A. STRUCTURE OF THE FLOWER

As an introduction to the study of the flower, no type is better suited for consideration than the flower of the marsh-marigold. The plant grows in almost every New England swamp, and its yellow flower clusters are a familiar sight in early spring.

Caltha belongs to the family *Ranunculaceæ* — a word which means "living with the frogs," since many members of the family are marsh plants. Fig. 61 should be correlated with the following description.

Let us note, first of all, that the flowers are borne on pedicels and stand in a slightly cymose inflorescence. At the base of each pedicel is a reduced axillating leaf or bract. The flower itself possesses radial symmetry; that is, the parts radiate from a central point as the spokes of a wheel radiate from the hub. The botanist calls such a flower *actinomorphic* or *regular*. Each flower is surrounded by a set of yellow members (*sepals*) which are much like one another; collectively they constitute the *perianth*. We need not search far to solve the question of their morphology, for they are shaped and veined like leaves, while

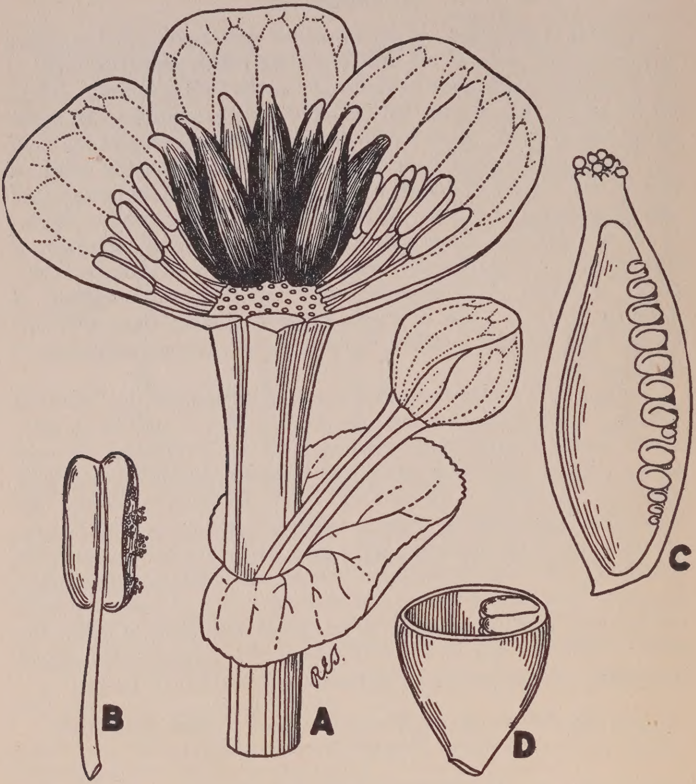

FIG. 61.— Study of Flower of the Marsh-marigold (*Caltha palustris*): A, flower and bud enlarged; B, single stamen; C, single carpel in longisection; D, carpel in cross-section.

the outer ones are even slightly greenish. Indeed, specimens are not rare in which the bracts (obviously leaves) also become bright yellow and are shaped like the sepals. The perianth of many flowers is differentiated into two sets of members — an outer, made up of green and bract-like leaves, called sepals, or collectively the *calyx*, and an inner, of colored members or *petals*, which collectively take the name of the *corolla*.

Botanists look upon the flower of *Caltha* as a very primitive type and believe that its lack of a double floral envelope is a primitive feature. When only one set of members is present, as in this case, we call it a calyx, or we may also say that the *Caltha* flower has a *haplochlamydeous perianth*. If there were both calyx and corolla we should call the perianth *diplochlamydeous*. The student may ask why we should call the bright members sepals and not petals. It must be confessed that the application of the term *calyx* to all haplochlamydeous perianths is a bit arbitrary, though in the *Ranunculaceæ* there is considerable evidence that a true corolla arose later in evolution by conversion of the outer members of the next row (stamens) into petals. *Caltha* is a primitive member of the family and still clings to old customs.

The perianth is primitive in another feature also: its sepals vary in number from four to eight, though five is the common number. In higher plants we find no such fluctuation in numerical plan.

If we pull away the sepals, it will be noted that they leave a set of small transverse scars behind and that these do not lie on the same level. This means precisely what it did in the case of the girdles of the horse-chestnut branch — we are dealing with a region of congested nodes and internodes.

Inside the perianth stands the *andrœcium*, consisting of dozens of stamens. The term *stamen* is an old one applied by early botanists to these organs and merely means "a thread." To the older botanists and to the layman, it is the male organ of the flower, and the idea is reflected in the term *andrœcium*. Stamens are not sex organs, however; their real nature can only be appreciated after a study of the lower plants from which the flowering plants evolved.

If we remove an unwithered stamen (Fig. 61, B) and examine it with a lens, we will find that it is differentiated into a basal thread-like *filament* and a terminal yellow *anther*. The latter consists of a middle *connective* (the continuation of the filament), and two elongate pouches called *anther-sacs* (also *pollen-sacs* or *loculi* or *cells*). Each sac is composed of two *locelli*. Along the side of each anther can be seen an indented line or cleft (*stomium*) through which the *pollen grains* sift out when the anther is mature. The single stomium serves for both locelli on one side. The stamens, like the sepals, are leaves, but they are leaves highly modified from their original condition and they bear *spore-sacs*. The proof that they are really foliar organs rests on a basis of comparative anatomy, of teratology, and of paleontology.

In Chapter I we learned that the spore-sac is one of the fundamental organs of the plant. Here for the first time we see it attached to its leaf. The great number of stamens of the *Caltha* flower is again considered to be a primitive floral feature, and once more we are impressed by the great number of nodes which must be involved in the axis of the flower.

If we remove the stamens, or take a fruiting axis from which they have fallen naturally, the low spiral of their phyllotaxy becomes evident from the arrangement of their scars. It should be realized that our own observations are proving to us that a flower is a branch with the leaves remarkably congested. The term *torus* or *receptacle* is applied to the floral axis upon which the floral members are seated.

There now remains at the top of the receptacle a small cluster of yellowish-green bodies which resemble tiny pea-pods. These collectively constitute the *gynœcium;* individually they are called *carpels*, or *simple pistils*. Each carpel is, in fact, a small pod with a basal swollen portion called the *ovary*, and a terminal beak with a slightly brownish and rough *stigma*. The ovary of a plant has absolutely nothing to do with the organ of the same name in animals. The name was originally applied through a misconception.

In many flowers there is an elongate *style* between stigma and ovary, but in the *Caltha* flower the stigma is practically sessile.

Upon opening a partly grown ovary with needles or razor, it will be found that the ovary contains two rows of tiny bead-like *ovules* fastened to its *ventral suture* (the one facing inward). These are destined to become seeds.

There is considerable evidence which goes to prove that the carpel is a leaf. If we imagine an ordinary flat, ovate leaf to bear ovules along its margin, and then think of it as folded longitudinally along its midrib, while its edges grow together and enclose its ovules, the result will be the carpel. Something like this appears actually to have happened in the ancient past.

All our modern seed plants which have ovules enclosed inside the carpellary leaf, just as they are in *Caltha*, are called *angiosperms* in contradistinction to those which have seeds borne naked on the carpellary leaf. The latter are called *gymnosperms*. Just as might be expected, the latter preceded the angiosperms on the earth. One of the most perplexing problems of evolutionary botany is to settle just how, when, and where the angiosperms originated from the gymnosperms. Evidence seems to point to the North Polar regions as the place of origin, and comparative anatomy can reconstruct the broad outlines of the course of this evolution, but the actual gymnosperm ancestors of the angiosperms are still unknown. Darwin called the problem "the abominable mystery," and so it still remains.

B. SUMMARY

Let us recapitulate the points brought out in our study of the morphology of the *Caltha* flower:

1. The actinomorphic flower is borne on a pedicel which springs from the axil of a bract.

2. The pedicel expands above into a conical receptacle or torus which is actually a congested stem with many nodes and internodes. Its elongate form is naturally a primitive feature.

3. The haplochlamydeous perianth or calyx is made up of a variable number of sepals, which are only modified leaves.

4. The andrœcium consists of many stamens, which are also modified leaves; each is composed of a filament, a connective, and two anther-sacs, cells, or loculi. Each anther-sac consists of two locelli which contain the pollen grains. The pollen escapes through a longitudinal cleft along each side of the anther. The stamens stand in a low spiral around the receptacle.

5. The gynœcium, made up of the individual carpels, or simple pistils, crowns the torus. The carpel is only a folded leaf; it is differentiated into ovary and sessile stigma. The ovary bears ovules inside along the ventral suture.

33. *The Functions of the Flower*

And now what is the use of all this elaborate mechanism, and how does it function? The flower is a device to insure the reproduction of the plant, and in most cases we may be quite sure that all the odd modifications are intended to attract insects in order that the latter may carry the pollen grains to other flowers and effect *cross-pollination.* To understand the meaning of the term, further description is necessary. While the pollen is being shed from the anthers, the stigma passes into a receptive condition; its rough surface often secretes a small amount of sticky fluid in which the pollen grains may be entangled. When the pollen grains land on such a stigma of their own species, they crack open and from each one a tube grows out. This travels down through stigma and style till it reaches an ovule in the ovary. Then it pierces the ovule through the micropyle and conveys into it two tiny masses of germ-plasm known as *sperm cells.* One of these unites with an *egg* (also a bit of germ-plasm) which lies deep inside the ovule. The union of egg and sperm constitutes *fertilization* or *zygosis*, and the fertilized egg is called a *zygote*. This zygote, then, represents a fusion of two bits of germ-plasm derived from male and female parents. It grows to be an embryo, just such as we studied in Chapter I.

All the display devices of the flower — color, nectar, perfume — are meant to attract insects to it in order that they may become the unconscious agents for the distribution of the pollen.

The whole subject, though seemingly so simple, is really very obscure. First of all, it is not true that cross-fertilization is necessary to all plants. Some get along perfectly well without it, and some even have special methods of sprinkling their own pollen on their own stigmas and thus effecting *self-pollination* with subsequent *self-fertilization*. But, on the other hand, some plants are dependent on cross-fertilization, since their own pollen will not send out tubes on their own stigmas.

Some botanists go so far as to say that Nature made a blunder when she evolved such elaborate cross-pollination devices, and that these were no sooner evolved than they were found to be useless. The entomologists also attack from another side by telling us that insects are very short-sighted and that the colored parts of flowers must be very ineffective as attraction devices. In general we may say that cross-pollination probably does insure somatic vigor, and, furthermore, that the mixings of germ-plasms may be a factor in bringing about variations in the progeny. There is evidence that new species may arise through such blendings.

34. *The Flower of* Trillium, *Lily Family* (*Liliaceæ*)

As an example of a flower which has progressed further in evolution than has *Caltha*, we may next consider the common red trillium or wake-robin (*Trillium erectum*) which is a member of the lily family. Fig. 62, however, is based on the tulip, which is a member of the same family and is very similar in floral details.

Trillium belongs to that ecological group of plants called tropophytes of which we have had occasion to speak before — those plants which store food in their underground parts, and flower and fruit in early spring while woodland conditions are favorable.

The stem of trillium bears three, rhombic-ovate, net-veined leaves, from between which there springs a single terminal flower. It is at once evident that the flower is built on a plan of three: three lanceolate green sepals, three lanceolate purplish-red petals, six stamens in two sets of three each, and a central gynœcium with three stigmas. The color of the petals is almost that of decaying flesh and the evil odor of the flower suggests that flies effect most of the pollination.

The gynœcium demands careful interpretation, for the carpels, instead of standing free from one another, are fused together to make up what is called a *compound pistil*, in contradistinction to the simple pistils of *Caltha*. Such a condition of fused carpels constitutes *syncarpy* while a gynœcium with free carpels, as in *Caltha*, is said to be *apocarpous*. The trillium flower, then, has a *syncarpous*, *tricarpellary gynœcium*. If the ovary be cut across, the three loculi can be seen, and

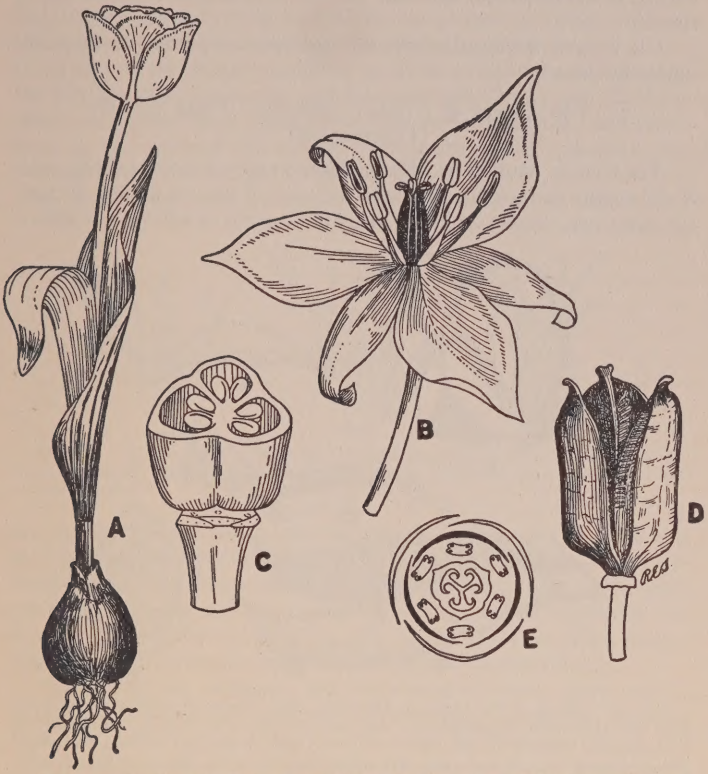

FIG. 62. — Study of the Tulip: A, flowering bulb; B, single expanded flower; C, tricarpellary ovary in cross-section; D, the capsular fruit; E, floral diagram representing the ground-plan of the flower. (B, C, D, E, redrawn from Baillon.)

in each are about four rows of ovules along the ventral suture. The fruit of the trillium is fleshy — that of the tulip, shown in Fig. 62, D, is a dry capsule.

It will be noted that the trillium receptacle is not conical like that of *Caltha*, but is flattened, and that the members stand in circles, not in spirals.

Let us now advance to a flower curiously adapted to cross-pollination by bees.

35. *The Flower of Cytisus racemosus, Pulse Family (Leguminosæ)*

The *Cytisus* plant is usually in bloom in greenhouses in spring, and it will supply us with a representative flower of the pea family, though the sweet-pea, illustrated in Fig. 63, will do quite as well since it differs in relatively slight details. The individual sweet-scented flowers of *Cytisus* are borne in drooping, short racemes and at first glance are quite different from those of either *Caltha* or *Trillium*. They are not built on the star plan (actinomorphic), but are *bilaterally symmetrical* or *zygomorphic*.

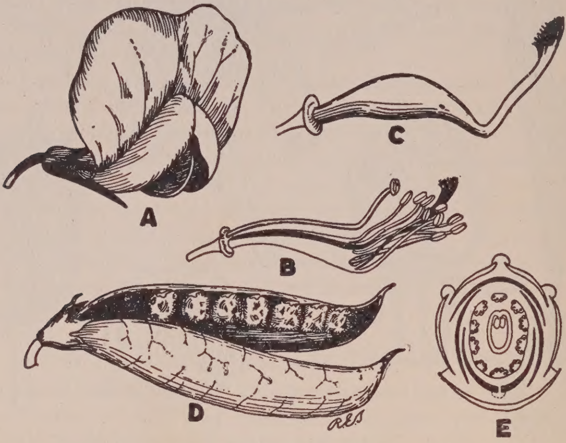

FIG. 63. — Study of the Sweet-pea Flower: A, single flower; B, androœcium enclosing pistil (the androœcium is *diadelphous* — one stamen is free from its nine "brothers"); C, gynœcium of a single carpel; D, opened fruit with seeds (a legume); E, floral diagram; it should be noted how union of sepals, of keel petals and of nine stamens is indicated. (Redrawn from Baillon.)

Let us look first at the calyx; it is small and tubular, and seems at first sight to have three points. A little study of the lower point, however, reveals the fact that there are really three sepals involved in it, but that they cohere lightly together. The calyx, then, consists of five sepals, but they have undergone *zonal growth.* Suppose one imagines a circle of five small calyx leaves beginning to develop from a growing point in exactly the same manner as described for the ontogeny of the leaf. After the points of the sepaline leaves are well developed, think of the circle of tissue on which they rest beginning to grow upward as a thin ring. As the ring grows higher, it can be realized that it will carry the sepaline points upwards, and the result will be just what we have seen — a tubular calyx. In a similar manner originate all such structures as the trumpet-like corollas of morning-glories, petunias, etc. Sometimes the stamens get carried up with the corolla tube and then they seem to rise from the corolla, or as the older books put it, they are *epipetalous* or inserted on the corolla. The most curious and striking zonal modification is one which involves the receptacle. Sometimes the edge of the receptacle grows up as a rim, carrying the perianth and stamens with it and leaving the gynœcium sunken at the bottom of a bowl or cup (Fig. 64, B). Such a flower is called *perigynous;* it is seen commonly in certain members of the rose family.

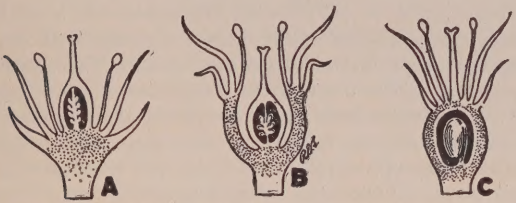

Fig. 64. — Modifications of the Floral Receptacle: A, diagram of the hypogynous flower — ovary superior; B, diagram of the perigynous flower; C, diagram of the epigynous flower — ovary inferior.

Sometimes the receptacle and the wall of the ovary grow up together and the union of receptacle and carpellary tissue is so intimate that the perianth and stamens seem to spring from the top of the ovary. Such a flower is called *epigynous* and the ovary is said to be *inferior* (Fig. 64, C). Now we need a term for the primitive types of flowers like those of *Caltha* and *Trillium,* which have undergone no zonal growth of receptacle; such a condition is logically called *hypogyny* and the gynœcium (either apocarpous or syncarpous) is said to be *superior* (Fig. 64, A).

To summarize the above matter:

1. The primitive flower is hypogynous and has a superior gynœcium; examples: *Caltha, Trillium, Cytisus.*

2. The perigynous flower has undergone zonal growth of the receptacle rim, hence the gynœcium is sunken in a cup on the edges of which perianth and andrœcium are borne; examples: the cherry flower and the plum flower.

3. The epigynous flower arises through zonal growth of receptacle and gynœcium wall. Hence the carpellary cells or loculi are enclosed inside the receptacle and the perianth and andrœcium seem to spring from the top of the ovary. Such a gynœcium is called inferior.

It will be obvious to the student that epigyny is a very advanced floral character. The most highly evolved of all dicotyledons, the *Compositæ*, are epigynous, though many other advanced families show the same condition.

To return to the *Cytisus* flower: we have seen that the calyx is tubular and five-toothed. Let us now observe the corolla. At the back stands a broad petal; on the sides are two others which are narrower and slightly concave, while below there is a compressed sac, shaped something like a boat flattened from side to side. This type of flower has been called *papilionaceous* from some fancied resemblance to a butterfly. If we take a fresh young flower and press lightly down on the boat-shaped structure in front, a surprising thing happens: out jump the stamens with explosive violence and away goes a puff of pollen into the air. If we note a honey-bee seeking nectar from such a flower it will be found that it always lands on this very region and that its weight sets off the catapult mechanism. Thus the belly of the insect is liberally powdered. Later it may go to another slightly older flower in which the stamens are withered but in which the stigma is ready to receive pollen, and thus cross-pollination is effected. A flower whose stamens mature before the stigma becomes receptive is called *proterandrous*. Such flowers have a sure method of avoiding self-pollination.

The petals of the pea type, such as the one we are now studying, have received special names. The big posterior one is called the *standard;* the lateral ones are called *wings;* and the lower one is the *keel.* In the *Papilionoideæ*, the tribe of the *Leguminosæ* to which *Cytisus* belongs, the keel is made up of two petals which have undergone development as one, but it is interesting to note that the fusion in *Cytisus* is not yet quite complete. In the *Cæsalpinoideæ*, a more primitive tribe of the family, the two keel petals are wholly separate.

If we remove the corolla, the andrœcium and gynœcium remain behind. With the lens it can be seen that the andrœcium consists of ten stamens which are all united at their base into one piece, but the filaments remain free in their upper part. The condition is obviously another result of zonal growth. The books speak of such a state as *monadelphy* and the stamens are said to be fused or united into a tube. This is not literally correct since they were never (ontogenetically) free, but such terms are convenient and avoid circumlocution. The sweet-pea has *diadelphous* stamens, viz., one remains free from its nine "brothers." If we slit the stamen tube open, the gynœcium appears. It looks like a miniature hairy pea-pod and has a long style and a capitate stigma. For the more intimate study of it we may just as well select a nearly mature fruit in which the ovary has enlarged; its style and stigma have possibly dried up and fallen away. Upon opening the ovary the maturing seeds are seen attached to the ventral suture; some may be abortive, since the eggs in them may not have been fertilized.

36. *The* Sunflower (*Helianthus annuus*), *an Example of a Composite Flower*

Highest of all dicotyledon families and dominating the flowering plants stands the family of the *Compositæ*, estimated to include about 13,000 species and more than 10 per cent of all the flowering plants. Many members of the family such as asters, goldenrods, daisies, etc., are known to everybody. The term *composite* refers to the fact that the seeming flower of such plants is really an aggregate of many tiny flowers, or florets, all borne together in a head on a conical or flat *disc* and surrounded by an *involucre* of congested bracts. The disc may be looked upon as derived from a condensed spike in which the axis has expanded laterally instead of elongating. Or it may have been derived from the congestion of an umbellate inflorescence.

If we examine the disc of the sunflower, it is evident that it is covered with scores of florets; those in the center, called *disc florets*, are small and tightly packed in alternating rows, while those on the periphery, called *ray florets*, look like yellow petals. Their corollas form long straps and together they resemble a fringe around the disc.

When we study the disc florets more intimately, we shall find them in three conditions as regards maturity. The inner ones are still in bud; the next rows are shedding pollen; while the outermost ones next the ray florets may have the style and two-pronged stigma exposed. Thus it is evident that anthesis proceeds centripetally and that the florets are proterandrous. Such centripetal anthesis on a flattened inflorescence axis is equivalent to acropetal anthesis on an elongated axis. If we break the disc, the florets will be seen to be interspersed with dry scales called *chaff*. These scales probably represent the axillating bracts of each floret of the inflorescence.

A single floret consists of an inferior ovary with a tubular five-toothed corolla on its top; outside the corolla are two small mem-

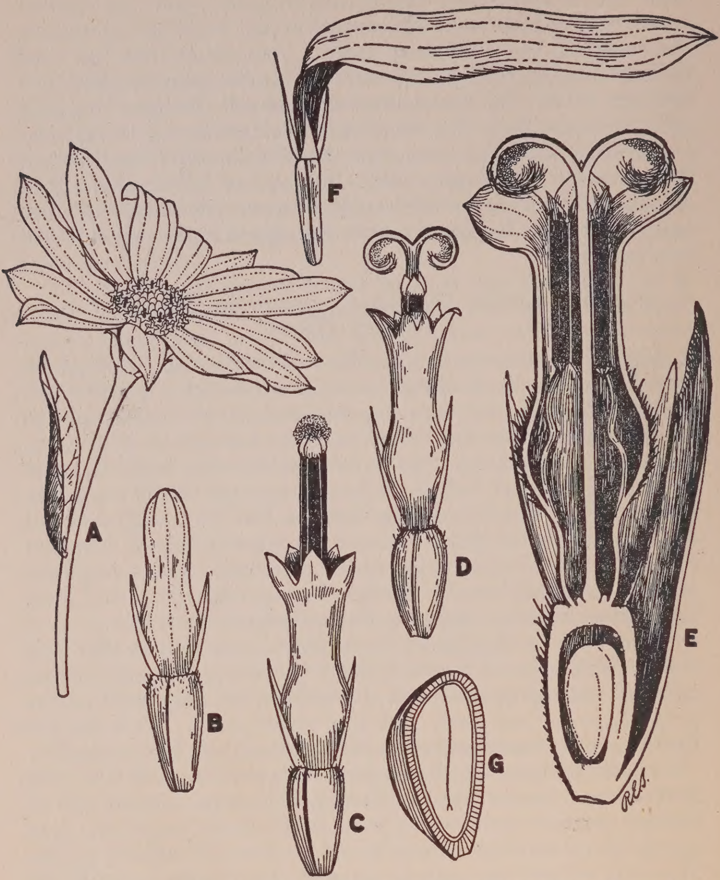

FIG. 65. — Study of the Sunflower: A, habit of sunflower head (*capitulum*); B, one of the disc florets in bud; C, disc floret expanded with stamen tube exserted and pollen exposed; D, disc floret with elongated style and reflexed stigmas; E, same stage as D enlarged to show details; F, ray floret whose strap-like display organ is formed of three fused petals; G, fruit (achene) in longisection showing large dicotyledonous embryo and absence of endosperm.

branous scales which probably represent a reduced calyx. In many composites the calyx consists of a set of bristles or plumose hairs which assist in the distribution of the fruit. When the corolla tube is split open, one sees five stamens attached to the tube. Their filaments are free, but their anthers are united. The pollen is shed inside this anther tube; the style then elongates and the hairy stigmas sweep the pollen upward and outward so that it may be exposed to visiting insects. This ingenious device constitutes the "*pollen presentation mechanism*"; the fuzzy stigmatic tips function something like a test-tube brush. Not till all the pollen has been pushed out do the stigmas expand, and thus self-pollination is avoided.

The structure of the ray florets is quite different from that of the disc florets. Their main function is display and they have given themselves so completely to it that they have lost both stamens and style. Hence they are unable to form seed and are sacrificed to the welfare of the colony. They arose in evolution from the modification of an outer row of disc florets; transitions between the two types are not uncommon in *Helianthus*. Thus the compositaceous flower illustrates the principle of *division of labor* among its florets — a principle which is also carried to great extremes in the social life of certain insects and to a lesser degree in human society.

Let us note how far the composite head (*capitulum*) has departed from the *Caltha* inflorescence. In *Caltha* the flowers were large and loosely arranged in a cyme; in *Helianthus* they are small and congested into a head whose disc seems to represent a flattened floral axis and whose involucre is composed of a congestion of bracts. The chaff on the disc seems to represent the axillating bracts of the individual florets. The *Caltha* flower is actinomorphic, hypogynous, and haplochlamydeous, with free sepals, many free stamens, and several free carpels which bear ovules on the ventral suture. The *Helianthus* disc floret is epigynous; it has a diplochlamydeous perianth, though its calyx is reduced to two scales; its five petals are united into a tube which bears the five stamens, whose anthers are united around the style (*syngenesious*); its carpels are reduced to two, and the ovary is inferior. There is but a single loculus in the ovary, since the wall separating the two carpels has been lost, and there is a single basal ovule.

Yet profound as these differences may seem to be, they are connected by a series of intermediate forms. The angiosperms are so recently evolved that almost all the forms which ever existed seem to have left descendants which are not much modified. Let us go beneath the surface of these facts and trace the activity of a deeper law.

The *Caltha* represents the archaic and original floral type. It is a self-sufficient system — a complete cosmos of protective, attractive, and reproductive parts. But as evolution progresses there is a manifest tendency to gather these unit flowers into denser inflorescences such as cymes, umbels, and heads. Thereupon they give up something of their former autonomy and begin to coöperate as units in a new system of higher degree. This tendency reaches its highest expression in the *Compositæ*, where the individual florets are integrated into a new and compound flower. In a curious manner the sunflower head simulates the simple flower of the buttercup. Its involucre is equivalent to a calyx, its ray florets resemble petals, its disc florets carry on the function of reproduction and are, in consequence, parallel to the stamens and carpels of the older flower. We are fully justified in calling it a flower of the second degree.

But the matter does not stop here. In many composites the compounding principle is once more at work and the heads themselves are drawing together into cymes, umbels, and capitula. This process reaches its acme in the globe-thistle (*Echinops*) whose primary involucrate heads are aggregated into secondary heads which are subtended by a second involucre. This is truly a flower of the third degree.

We are dealing with one of Nature's basic principles of construction — a principle which gathers together the units of one system and builds up larger systems, which, in their turn, are compounded into systems still higher. Strangely, too, the higher systems are generally copies of the lower, just as the sunflower is a copy of the buttercup. Hence came a familiar aphorism of the Hermetic philosophers: "As above, so below."

37. *The Flower of the* Rye (*Secale cereale*), *Grass Family* (*Gramineæ*)

The rye, *Secale cereale*, is the last flower which we shall consider in detail. It stands on quite another line from the sunflower and seems to have been derived from a lily type. Fig. 66 is based upon the flower of the oat, which is very similar.

The flowers of the rye — called florets — are borne in pairs on short lateral axes, and the whole structure (two florets and tiny axis) constitutes a *spikelet*. The spikelets in their turn are arranged along the opposite sides of a slightly zigzag main rachis to form a spike. The inflorescence of the oat is a panicle.

The spikelet is considered to be the unit of the grass inflorescence, and the classification of the grasses is largely based upon it. Many grasses bear more florets per spikelet than does the rye, but there is an interesting piece of evidence that the rye spikelet, too, was once more complex, for if we separate the two florets and look between them we will see a slender bristle whose tip bears a tiny rudiment of another

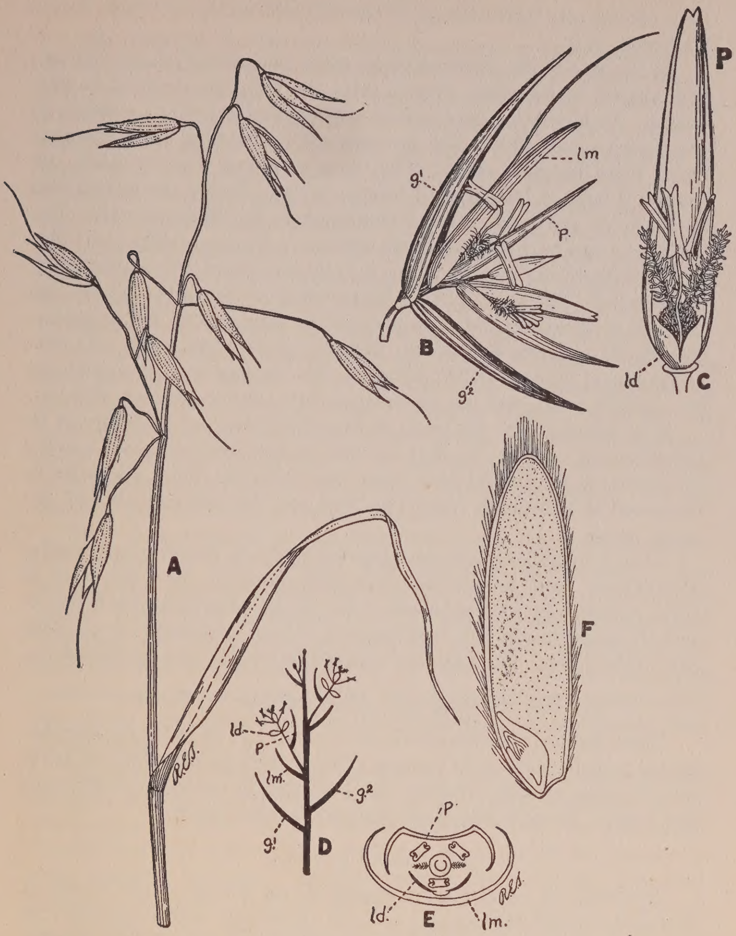

FIG. 66. — Study of the Oat Flower: A, paniculate inflorescence of the oat; B, single spikelet bearing two perfect and one abortive flowers (g^1 g^2, first and second glumes; *lm*, lemma; *p*, palea); C, single floret with lemma removed showing bicarpellary ovary with plumed stigmas, three stamens, lodicules (*ld*), and palea (*p*); D, diagram of oat spikelet (lettering as in B and C); E, diagram of oat floret; F, fruit (a caryopsis) in longisection showing embryo and endosperm. (B, C, E, F, redrawn from Baillon.)

floret. This bristle is the elongated lateral axis, and atavistic conditions are not rare where instead of the normal two, three or more florets are borne on it.

At the base of the normal spikelet stand two narrow, sharp-pointed, boat-shaped scales called *glumes;* their sole function seems to be protective. Inside each glume stands the fertile floret which consists of two scales — one dorsal and one ventral — enclosing three stamens and a pistil between them. The outer or dorsal scale is called the *lemma;* it bears a long barbed bristle or *awn.* Inside the lemma and facing it lies the *palea,* a more membranous and delicate scale. The three stamens bear long greenish anthers, and at maturity their filaments elongate and push them out into the air, where they dangle freely in the wind. The small pistil is bicarpellary; it bears two plume-like stigmas, a device related obviously to the wind-drifted pollen grains. Outside the stamens lie two tiny, delicate, transparent scales with fimbriate edges; they are called *lodicules.* The bicarpellary pistil encloses but a single ovule, and the whole ripens into the rye grain or *caryopsis.*

It is believed that the parts of the grass flower are homologous to the following ones of the lily: the two glumes are two basal bracts; the lemma is the special bract associated with the floret; the palea is composed of two sepals fused together; and the lodicules are two reduced petals.

Thus we conclude our introductory study of flower types, realizing that we have become familiar with some of the basic facts of floral morphology and have seen a few of the principles which are at work to mold flowers into a richness of variety surpassed by no other part of the plant. We may now proceed to a more general discussion.

38. *The Evolutionary Modifications of Flowers*

Three general principles seem to be at work in effecting the morphological transformations of flowers. One of these we may call the tendency to zonal growth; another the principle of economy of material; and a third, the principle of adaptations to insect visits.

A. ZONAL GROWTH

Tendency to zonal growth affects all the whorls of the flower; it produces tubular calyces and corollas (synsepaly and sympetaly); it causes the stamens to assume the conditions of monadelphy, diadelphy, etc.; it produces syncarpous gynœcia, and finally, invading the receptacle, brings about perigyny or epigyny. In some cases zonal growth also effects economy of material. For instance, an inferior ovary need not build up thick carpellary walls, since it is imbedded in the flesh of the protective receptacle.

B. THE PRINCIPLE OF ECONOMY

The principle of economy is usually evidenced by suppression. If one of the perianth whorls be suppressed, the result is a haplochlamydeous perianth, though it is sometimes impossible to say whether such a condition is due to suppression or to a primitive state of undifferentiation. In *Caltha* it is probably the latter. If all the perianth be suppressed, the flower is said to be naked or *achlamydeous.* If the androecium be suppressed, the result is an *imperfect flower*, and in this case it would be called *pistillate* or "*female.*" If, on the contrary, the gynœcium be suppressed, the flower becomes *staminate* or "*male.*" Plants with imperfect flowers are said to be *diclinous.* If the staminate flowers are on one plant and the pistillate on another, they are said to be *diœcious* — a condition which is found, for example, in the willows. If, on the other hand, the staminate and pistillate flowers occur on the same plant but in different inflorescences, the plant is *monœcious* — a condition found in the castor-bean, in alders, birches, oaks, etc. If both androecium and gynœcium be suppressed, the result is a *neutral flower* whose only function is for display purposes to attract insects to an inflorescence whose perfect flowers may be very small. The ray florets of the *Compositæ* are often neutral.

The "double flower" of the florist is a type in which the reproductive energy has been diverted into vegetative development. The stamens and even the pistils transform themselves into sterile colored leaves. When these are derived from sterilized stamens they are often called *staminodia* and in many cases one may find rudimentary anthers attached to petaloid growths. It should be realized that such double flowers are all monstrosities, and at the limit of transformation when their reproductive organs are completely metamorphosed they are worthless to the plant.

Suppression of ovules in the carpels is a common phenomenon, and all stages of ovule abortion may be found in a family of plants. In the *Ranunculaceæ*, *Caltha* matures many seeds per carpel; the goldthread (*Coptis*) has only four to eight seeds per carpel, while the buttercup itself matures but one. Another feature characterizing advanced families is a tendency to abort the inner carpellary walls; the primrose, for example, has a pentacarpellary gynœcium, but there is but one cavity inside it.

C. MODIFICATIONS TO FACILITATE POLLINATION

Adaptation to insect visits is particularly manifested by modifications of symmetry from radial (actinomorphic) to bilateral (zygomorphic) or even asymmetrical.

As explained under *Caltha*, the great majority of flowers are adapted to cross-pollination. The transference of pollen necessitates some kind of moving agents, and plants have taken advantage of all that were available. Pollination by wind, water, and insects is most common, though a few cases are known in which birds, bats, and even snails are the agents concerned.

(1) *Anemophilous Adaptations.*

The terms *anemophilous*, *hydrophilous*, and *entomophilous* are applied to the first three types of flowers, that is, to those which "love" wind, water, and insects respectively.

Wind-pollinated flowers are commonly greenish, since there is no necessity for attractive colors; their flowers, too, are often small and borne in dense inflorescences. As examples may be mentioned the flowers of grasses, sedges, cat-tails, and many early-flowering forest trees such as conifers, chestnuts, and oaks. Their pollen grains are minute and borne in remarkable abundance, since the wind is very wasteful, transporting one grain properly to a stigma while it wastes millions of others. Some wind-borne pollen grains are provided with special buoyancy devices — the pines and spruces are good examples. Sometimes in the spring the surfaces of pools become covered with yellow dust which country people call "showers of sulphur." The "sulphur" is really pine pollen; it drifts about for some time and finally sinks down into the muck below. This is a phenomenon of great interest and significance, since it illustrates what took place on a tremendous scale in ancient days. In the Carboniferous Period there flourished great forests of giant trees quite unlike any now living. They shed from their cones vast quantities of spores, which, collecting in open water, finally sank down and became combined with other plant debris such as leaves, branches, etc., to form coal. Bituminous coal consists of just such materials compressed and slightly modified in chemical composition.

(2) *Hydrophilous Adaptations — The* Hornwort *and* Eel-grass.

Hydrophilous flowers are naturally confined to water plants. By way of illustration we may describe the flowers of the hornwort (*Ceratophyllum*) and the eel-grass (*Vallisneria*).

The ceratophyllums are submersed plants with dissected leaves, and grow in rather deep water. The flowers are monœcious and stand in the axils of the leaves. The pistillate flower consists of a small, green, toothed calyx with a single carpel; the staminate, of calyx and twelve to sixteen stamens. The stamens each bear two pollen chambers, but the upper part of each chamber is filled with air. At maturity the stamens break out of the calyx and, rising to the surface of the water, shed their pollen grains. The grains are slightly heavier than the water, hence they sink slowly downward to the stigmas.

Vallisneria, the fresh-water eel-grass, has a remarkable pollination mechanism. The plant roots in the mud of shallow ponds, and its long tape-like leaves are wholly submersed and supported by the water (Fig. 67). The pistillate flowers are borne on very long string-like peduncles and expand at the surface of the water. They have three stigmas which recurve outward beyond the perianth. The staminate flowers are borne on spikes underneath the water. Just before anthesis the staminate buds break off and rise to the surface, where they open and proceed to float about on their three boat-like sepals, holding their two pollen-covered anthers well up in the air. The wind drifts them into the surface-tension depressions around the pistillate flowers; then their anthers come in contact with the stigmas and pollination is accomplished (Fig. 66, E). The peduncle of the female flower then coils up into a spiral and pulls the ripening fruit down into the mud.

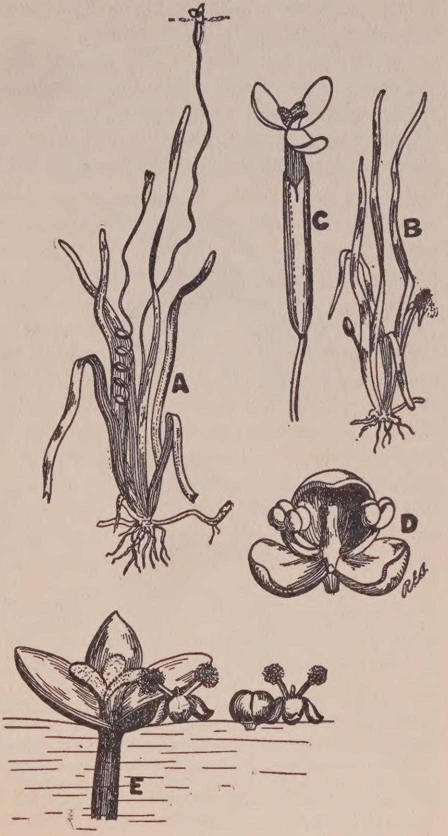

FIG. 67. — The Eel-Grass (*Vallisneria spiralis*): A, habit of pistillate plant; B, habit of staminate plant; C, pistillate flower enlarged; D, staminate flower enlarged, showing two stamens and an abortive pistil; E, the pollination of the eel-grass.

(3) *Extreme Entomophilous Adaptations.*

We are already familiar with some of the modifications by which flowers manage to press insects into their services. But to make the matter even more striking, let us describe a few extreme types which offer many puzzles to the botanist.

a. Orchids and insects. The orchids are the most highly evolved members of the *Monocotyledoneæ;* their flowers are often brilliant with color and extremely complicated in structure. A common native orchid is *Cypripedium acaule*, the pink lady's-slipper. The pouch of this flower is a singularly modified petal in whose front is a slit with inrolled edges through which a bee may enter. Once inside, the only way of egress is to squeeze under the stigma and out through a small round opening on either side, in the top of each one of which hangs an anther filled with viscid pollen. As the bee emerges the pollen is smeared over the dorsal side of the thorax and will be rubbed off on the stigma of the next flower visited.

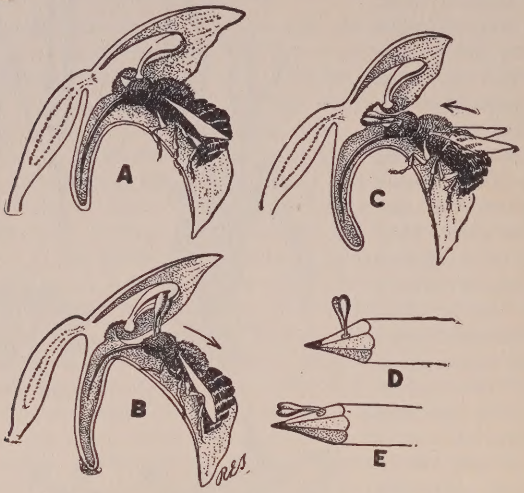

FIG. 68. — The Pollination of the Showy Orchis (*Orchis spectabilis*): A, a bumble-bee has entered the flower and is feeding on the nectar in the spur; the head is crowded up against the sticky discs attached to the pollen masses; B, the insect is leaving the flower and the stipitate pollen masses are being torn from the anther-sacs; C, insect about thirty seconds later entering another flower; the pollen masses have revolved to such a position that they are being thrust against the hollow stigma; D, pollen masses removed on a pencil-point; E, the same about thirty seconds later. (Adapted from Gibson.)

More remarkable still is the pollination device of the native showy orchis (*Orchis spectabilis*). A very similar mechanism characterizes the habenarias or rein-orchids also. In these flowers the anther contains two waxy masses of pollen, each of which is attached to a stipe which ends in a sticky disc. As the insect crowds into the flower to feed on the nectar which is contained in a posterior spurred petal, the glutinous discs meet it head-on and stick to the eyes or other parts of the face (Fig. 68, A). Then as the insect backs out of the flower, the pollen masses (*pollinaria*) are dragged out of the anther (Fig. 68, B). It will be observed that they stand upright — almost at right angles to the horizontal plane. Now should they remain in this position, it is clear that they would be thrust against the sticky disc of the next flower visited. And here lies the marvel of the device. Within thirty seconds the viscid disc attached to the insect's face has so contracted on its lower side that the axis of the pollinarium has swept through an angle of almost ninety degrees and lies horizontally *in just the correct position to be pushed against the sticky stigma of another flower* (Fig. 68, C, D, E).

b. The yucca and its pollination. Another puzzling pollination event is found in the *Yucca* flower. The yuccas or Spanish bayonets are plants of dry soils of the arid Southwest. They bear harsh, bayonet-like leaves from among which rise tall flower stalks bearing panicles of creamy, bell-shaped flowers. The yucca flower is pollinated by a special moth called the *Pronuba*. The female insect flies to the open flower where she molds a small ball of pollen and then runs up the style and crowds the pollen ball into the cup-shaped stigma. This may be repeated several times, or she may even carry the pollen ball to another flower. Finally she climbs down again to the ovary, thrusts her ovipositor through the carpellary wall and lays her eggs in the ovules. The pollen grains which she had placed on the stigma send down their tubes, the seeds begin to develop, and the larvæ of the pronuba feed on the growing seeds. Some seeds always escape destruction, and thus the yucca plant gains even if it does have to sacrifice part of its seeds.

We call such unreasoned adaptational activities as this of *Pronuba* by the name of instinct, but the term explains nothing.

c. The fig and its pollination. Even more marvelous and inexplicable is the pollination of the fig (Fig. 70). The fig fruit is an enlarged and hollow inflorescence axis, and the small "seeds," as we ordinarily call them, are really the carpels which belong to hundreds of tiny flowers which line the interior. The whole structure is called a *synconium*. At its larger end there is an opening leading to the hollow interior, and pointing inward around the opening are many small, sharp scales. Fig synconia are diœcious. One sort contains pistillate flowers only; the other sort (called a *caprifig*) contains two kinds of flowers. Those in the lower part of the synconium possess short-styled rudimentary pistils which never mature, while those above are definitely staminate.

Pollination is effected by a small wasp (*Blastophaga glossorum*). Suppose we start with a female wasp recently escaped from a staminate synconium or caprifig and consequently covered with pollen. She may fly to a pistillate synconium. As she creeps into it, her wings are often torn off by the many sharp scales. She wanders around among the pistillate flowers attempting to lay her eggs in the ovaries, but this is prevented, since the length of the styles interferes with oviposition. After inadvertently effecting pollination, the wasp dies. The seeds develop inside the carpels, and the synconium becomes the juicy fig of commerce.

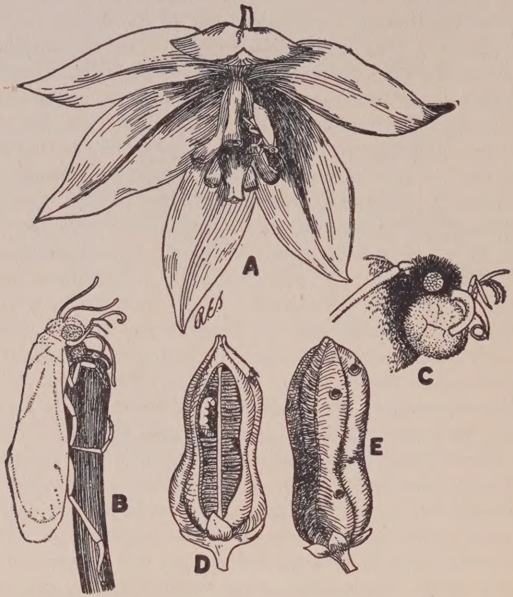

FIG. 69.— Pollination of the Yucca: A, single flower with *Pronuba* resting on pistil; B, *Pronuba* gathering pollen ball from anther; C, head of *Pronuba*, much enlarged, showing pollen ball which is used for artificial pollination of the stigma; D, ripening capsule with *Pronuba* larva feeding on seeds; E, ripe capsule, showing holes through which the insects have escaped. (A, B, D, E, adapted from Riley; C, from Trelease.)

But suppose the female *Blastophaga* enters another caprifig. The abortive ovaries at the bottom of the synconium have short styles, and she can easily lay her eggs. Then these abortive pistils, entirely useless to the plant, develop into small galls in which the *Blastophaga* larvæ live until maturity, when they escape from the galls and mate inside the synconium. Strangely enough, the stamens which lie in the upper part of the synconial pouch have so timed their maturity that just as the insects begin to escape they are shedding pollen. As a consequence the females, as they leave the synconium, are dusted with pollen and fly away ready to carry on the life history. Furthermore, a new set of pistillate synconia has so timed its development that it is ready to receive the insects.

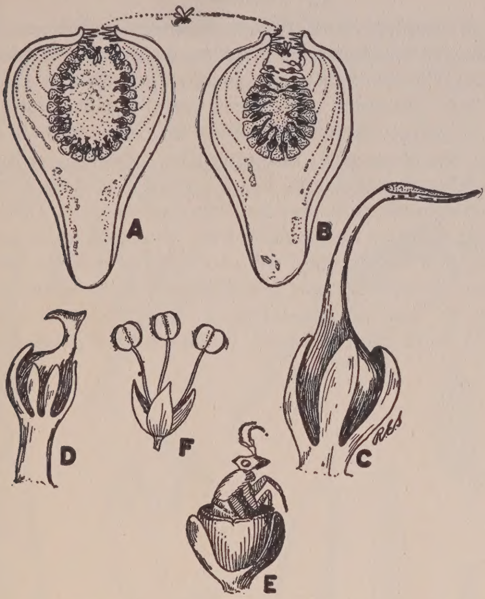

FIG. 70. — The Pollination Mechanism of the Fig: A, male synconium (caprifig) with gall flowers (rudimentary pistils) below and staminate flowers above. A female wasp is shown flying to B, the female synconium, in which the wasp dies after effecting pollination. C, fertile pistillate flower from female synconium; the length of the style prevents the wasp from ovipositing; D, rudimentary pistillate flower from male synconium (caprifig) in which the wasp lays an egg; it becomes a gall from which a wasp of the next generation subsequently escapes; E, wasp escaping from a gall flower; F, staminate flower. (Adapted from various sources.)

We cannot even attempt to explain the evolution of such a symbiotic system. When we realize that half the wasps are sacrificed in female synconia and half the flowers (caprifigs) never set any seeds, and that the life history of the flower is synchronized to the life history of the wasp, we can understand that we are at the boundary of sense knowledge where science gives way to metaphysics.

39. *Summary*

Thus we complete our introductory studies on flowers. We began with a primitive, indefinite, dicotyledonous type, *Caltha palustris;* we then advanced to the monocotyledonous *Trillium* and observed how evolution had produced a mathematically regular flower; *Cytisus racemosus* introduced us to zygomorphy and zonal growth; *Helianthus annuus*, to the phenomena of aggregation, epigyny, reduction, and division of labor among florets. Finally, the flower of rye illustrated for us a case of extreme reduction and wind-pollination. Then in a very brief and general way we considered the principles which are molding flowers into new forms: these seem to be zonal growth, the principle of economy of material, and modifications to facilitate pollination. Of the last we took up adaptations to wind and water, and finally described in detail a few symbiotic relationships of plants and insects.

CHAPTER VII

THE FRUIT AND SEED

With the subject of the fruit and the seed we complete the circle of our studies and come back to where we started; for the seed is at the same time the biological end of one generation and the beginning of another.

40. *The Kinds of Fruits*

The pistil matures into the fruit; hence a fruit is a mature gynœcium sometimes attached to accessory parts which fall away with it. Fruits may be *dehiscent* or *indehiscent;* that is, they may split open at maturity or remain indefinitely closed. Their walls (*pericarp*) may be dry or may become fleshy. Fig. 71 represents several types of dry fruits.

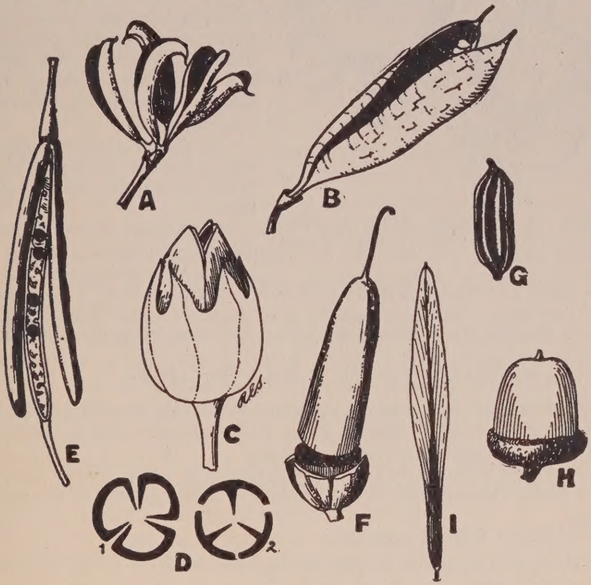

FIG. 71. — Common Dehiscent and Indehiscent Dry Fruits: A, follicles of *Cercidophyllum japonicum;* B, legume of *Baptisia australis;* C, capsule of tobacco; D, diagram of (1) septicidal dehiscence, (2) loculicidal dehiscence; E, silique of turnip; F, pyxis of plantain; G, achene of an umbellifer; H, cupulate nut of red oak; I, samara of ash.

A. *Follicle:* a pod which ripens from a single carpel and dehisces along one suture. The apocarpous gynœcium of *Caltha* ripens into a cluster of follicles.

B. *Legume:* also the product of a single carpel, but splits along both sutures and forms two valves. Most members of the pea family possess this type of fruit.

C. *Capsule:* the product of a compound pistil. A capsule may dehisce by splitting first into its constituent carpels, each of which dehisces secondarily along the ventral suture. This constitutes *septicidal dehiscence* (Fig. 71, D 1). On the contrary, the capsule may open through the dehiscence of each carpel directly into its loculus; that is, each carpel may split down the dorsal suture. This is *loculicidal dehiscence* (Fig. 71, D 2).

E. *Silique:* a kind of capsule which is long and narrow and possesses two parietal placentæ. It dehisces by two valves and often has a partition through it. The silique is very characteristic of the mustard family.

F. *Pyxis:* another capsule type which possess circumscissile dehiscence, so that its top falls off like a lid.

G. *Achene:* a small, dry, indehiscent, one-seeded fruit.

H. *Nut:* much like an achene but larger and usually the product of a compound ovary in which but one seed develops. The nut is sometimes surrounded by an involucre or cupule.

I. *Samara:* an indehiscent, one-seeded, winged fruit.

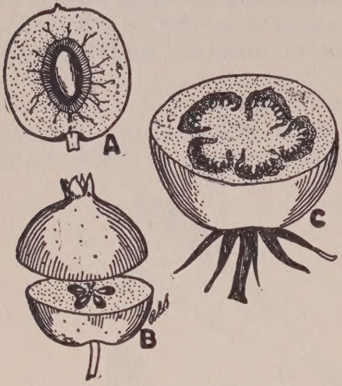

Fig. 72. — Common Types of Fleshy Fruits: A, drupe of peach; B, pome of apple; C, berry of tomato.

Fig. 72 shows three, common fleshy-fruit types.

A. *Drupe* or *stone fruit:* the product of a single carpel (usually) with its pericarp differentiated into an outer, fleshy *sarcocarp* (or *exocarp*), and an inner bony *sclerocarp* (*endocarp*) or *stone*.

B. *Pome:* a fleshy fruit with cartilaginous or bony carpel walls enclosed by a fleshy exocarp with is the product of zonal growth of the receptacle tissue.

C. *Berry:* fleshy throughout.

The term *aggregate* is applied to fruits such as those of the blackberry and magnolia, in which the ripened carpels of a single flower cohere and fall in a mass.

Accessory fruits are those "of which some conspicuous portion of the fructification neither belongs to the pistil nor is organically united with it except by a common insertion." The strawberry possesses such a fruit, for the fleshy, edible part is the curiously enlarged receptacle over which multitudes of achenes are scattered.

Multiple fruits are those which result from the massing together of the products of several separate flowers; they are inflorescence fruits. The mulberry possesses such a fruit, as does also the pineapple.

41. *Fruit and Seed Distribution*

It is clear that if seeds fell directly beneath the parent plant they would have a poor chance of growing up, since the struggle for existence is so keen. Hence, all sorts of devices are utilized to effect their distribution. It is sometimes the fruit and sometimes the seed that is adapted to spreading the species over the earth. Just as in the case of pollen-dispersal, any moving agent can be utilized: wind, water, animals, and even direct catapult mechanisms provided by the plant itself.

Wind-distributed fruits may be enclosed in bladdery husks and be rolled over the ground; such are the bladder-nut (*Staphylea*) and the husk tomato (*Physalis*). In this connection, too, should be mentioned the tumbleweeds. The term is applied to any richly branched and more or less globose herb which in autumn breaks away from its root and, heavily loaded with seeds, is tumbled about by the wind. Tumbleweeds stacked against fences are a common sight on the western prairies. Other wind-distributed fruits or seeds utilize the principle of the airplane, or better the glider. As they flutter slowly downward, they may be blown some distance from the parent. Familiar examples are the maple key and the samaras of the ash, elm, and linden. In the case of the catalpa, it is the seed, not the fruit, which is provided with fimbriated planes.

Most perfectly adapted to the wind are the hosts of plumed fruits and seeds, such as the fruits of many composites (dandelion, thistle, etc.) and the seeds of milkweeds, cottonwoods, and willows. Plumed or comose propagative bodies drift very long distances. For instance, it has been found that the fruits of the dandelion remain drifting indefinitely in relatively dry air with a wind of only about two miles per hour. The seeds of certain orchids weigh only .00000565 milligram and can be swept about the earth like fine dust.

Water is also effective in dispersal. Some fruits like those of the bur-reed (*Sparganium*) have spongy, air-filled pericarps; the cocoanut in its husk is carried by sea-currents from one tropical island to another.

Animals may act as dispersive agents in either one of two ways: they may eat the fruit and the seeds may pass unharmed through the alimentary canal; or they may carry fruits and seeds fastened to their hair. We have had already an illustration of the former group, for the seeds of the mistletoe are spread by birds which eat the berries.

Whenever a fruit is conspicuous or brilliantly colored and edible, one may be sure that the modification is intended to attract fruit- or seed-eating animals or birds. Fruits and seeds destined to be spread through becoming entangled in the fur of animals are provided with grappling organs which are of very diverse morphology. In the burdock (a composite) the involucral bracts bear hooked prickles; in the beggar's-ticks the barbed bristles are probably modified sepals; in the desmodiums the carpel walls are covered with tiny, hooked hairs; while in the unicorn plant the style develops into a great hooked beak.

Dispersal by a catapult mechanism occurs in the witch-hazel, in the balsam or touch-me-not, in wild geranium, and in other plants. In such cases the ripe fruits develop tensile stresses, then suddenly explode and hurl out the seeds, often to a distance of several feet.

CHAPTER VIII

THE HISTORY OF BOTANY AND THE PRINCIPLES OF CLASSIFICATION

Our introductory study of the plant body and of its morphological transformations incidental to ecological adaptations is now finished, and in the succeeding work we shall find that we are equipped with the knowledge requisite to the identification of the wild plants of field and woods.

Every man who pushes his studies very far is faced with the problem of establishing order among an ever-increasing set of ideas. Thus it is in botany; for when we come to realize that there are some 250,000 species of plants now known,* we begin to see how essential it is to introduce some scheme of classification among them.

There are two kinds of classification, known respectively as artificial and natural. The former picks out some common character which various organisms possess and puts these in a single group. For example, one might put all green-pigmented organisms together. Then the list would include plants, caterpillars, grasshoppers, frogs, and parrots. Of course this is an absurd illustration, but we shall soon see that the early biologists dealt for a long time with classifications scarcely less wild. Artificial classifications, however, still have their place, and are often used in modern keys for the determination of species.

The natural classification is an attempt to establish the actual blood relationships of plants. The botanist tries to reconstruct the phylogenetic tree, placing each group of closely related plants in a genus, a family, or a higher category. This constitutes the work of modern systematic botany.

42. *Plant Knowledge among Ancient People*

To the people of ancient times the need of systems of classification was not so pressing since they knew but a few easily recognized plants, mostly those of economic value. We know that nations whose records are almost obliterated carried on an extensive horticulture and were familiar also with many medicinal plants. The prehistoric lake-dwellers of Switzerland cultivated, among other things, wheat, barley, spelt, apples, water-chestnuts (*Trapa*), and even the curly-dock, which they used as a salad. Remains of all these food plants have been found in their kitchen-middens. The ancient inhabitants of Peru built terraced gardens on the mountain-sides, with remarkable supporting walls of masonry, and established elaborate irrigation systems; the Aztecs had fine gardens in which they grew not only vegetables and fruits but also flowers for decoration and for the altars of the gods. We even read of their shops in which one might buy hot chocolate. The Egyptian, Babylonian, and Assyrian gardens are all famous in legends. In a tomb of the Greco-Roman period in the Egyptian Fayum district, Professor Petrie found the remains of funeral banquets and of funeral wreaths in a perfect state of preservation. The plants used in the wreaths represented some twenty species, some of which are not natives of Egypt but must have been cultivated in gardens. They included the laurel (*Laurus nobilis*), myrtle (*Myrtus communis*), linden (*Tilia europœa*), mignonette (*Reseda odorata*), berries of the bittersweet (*Solanum Dulcamara*) strung on palm fibers, white water-lily (*Nymphœa Lotus*), and jasmine (*Jasminum Sambac*).

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* J. H. Schaffner, in *Ohio Journ. Sci.*, xxvii, 249.

The funeral feast had consisted of barley, wheat, cabbage, lentils, lupines, beans, peas, onions, grapes, almonds, peaches, cherries, pomegranates, walnuts, hazelnuts, and mulberries.

From Egyptian and Assyrian sculpture, too, we realize that plants such as the lotus, the papyrus, and the date very early gave motifs to decorative and religious art.

43. *Botany among the Greeks*

Our first glimpse of plant lore among these "superb ancients" comes down to us associated with the *Rhizotomi*. The word means "root-cutter"; these men were the doctors and magicians of old Greece. As we have learned, the word *pharmakon* signifies not only "drug" but also "magic." The *Rhizotomi* believed that the healing potencies of plants depended in no small degree upon their magical properties, and furthermore that these properties could only be conserved when the roots were gathered with magical precautions and ceremonies. Sometimes the collector must face to the east and mutter incantations; sometimes he must draw the tip of a sword three times around the plant; again, he must be anointed with oil. Some plants must be collected in the light of the moon, others in the dark (cf. "slips of yew slivered in the moon's eclipse," in *Macbeth*). This lore lasted a long time in the world, and an interesting survival is seen even to this day in the firm conviction of some gardeners that certain seeds must be planted and crops gathered according to the phases of the moon.

One of the most famous of the Greeks was Aristotle, (384–322

B.C.), who wrote a whole compendium of human knowledge. It is known that certain of his books dealt with plants, but these have been lost. His zoölogical treatises are of great merit and show the man as an original researcher into the world of natural phenomena.

The title "Father of Botany," however, was given by Linnæus to one of Aristotle's pupils, Theophrastus. This brilliant scholar was fifteen years the junior of Aristotle and like his master was a keen observer of nature. He directed his investigations to plants and made thorough morphological studies of them, even advancing as far into the fields of physiology and anatomy as the means at his disposal permitted. He has left us a list of about 500 species which he knew. For these plants the common everyday names familiar to horticulturists and doctors are used; thus, for a plant with many leaves, what could be more appropriate than the name *Myriophyllum?* For one with hard, stony seeds, the name *Lithospermum* is logically employed. The Greeks, moreover, were a fanciful and poetic people and had many folk-legends associated with plants. The daffodil (*Narcissus*) arose from the dead body of the youth who fell in love with his own reflection; *Iris* was the flower of the rainbow goddess, since it carried her colors. Theophrastus takes over all these names, with no idea that he is establishing a system which will be carried forward through the centuries. Aristotelian botany persisted to as late a date as the sixteenth century. Albertus Magnus (1193–1280) and Andrea Cæsalpino (1583) were its greatest exponents.

The Romans went to school to the Greeks and learned their botany from Theophrastus and later, lesser men. The cultures of Europe rest on the cultures of Greece and Rome. So the old Theophrastian names have come down to us. One need only open a modern manual of botany to realize that the dead hand of Theophrastus rests on nomenclature. We still use the generic names *Myriophyllum*, *Lithospermum*, *Acanthus*, *Cenchrus*, *Cyperus*, etc., all Theophrastian names. And more than this, so strong was the influence of the Greeks upon the science of biology that we even go to the familiar Greek sources for names of new plants.

The Arab scholars, too, deserve a word. We are indebted to them for preserving the writings of many learned Greeks and Romans during a period of fanaticism and barbarian inroads in Europe.

44. *Botany among the Romans*

As Greece declined, Rome began to rise, and slowly the center of culture passed westward. From Greece there came to Rome about A.D. 50, in the time of Nero, a famous physician named Dioscorides. As an applied scientist he gained great renown. Dioscorides knew about 600 plants, which he loosely classifies according to medicinal, aromatic, edible, and other qualities. It is said, however, that he recognized certain natural plant groups such as umbellifers, labiates, and legumes. His influence dominated medical botany for many centuries, and as late as 1500–1600 Latin commentaries on Dioscorides were numerous and were regarded as almost the last word in medicine. His works were translated into Spanish, French, Italian, and German.

In Vienna there is a famous manuscript copy of Dioscorides which was prepared for Juliana Anicia, the daughter of Emperor Flavius Anicius, about the beginning of the sixth century. It contains beautifully executed and lifelike drawings of medicinal plants.

The Romans themselves were a practical people and devoted their energies to establishing order through the world. From a botanical standpoint the name of Pliny the Elder (A.D. 23–79) should be mentioned. He was a prodigious worker and a most versatile man. His great literary monument is a *Historia naturalis*, of which volumes XII to XXVII dealt with horticulture, medicine, and agriculture. Pliny's work is not original, but is in the nature of a compilation of all existing knowledge. This gifted scholar met his death while studying an eruption of Vesuvius at close range.

Another celebrity of antiquity was Galen, a Greek, born in the year A.D. 131. From the age of seventeen till he was twenty-eight he traveled through most of the known world and in A.D. 164 came to Rome as physician to Marcus Aurelius. Galen was a man of wide medical learning who broke away from the slavish following of authority and advised his students to study plants at first hand, not from books. He placed small reliance on written descriptions of plants and taught by word of mouth and by demonstration. As a consequence we have little more than traditions concerning his work.

45. *Botany since the Renaissance*

As Rome began to decline in her turn, all learning entered a period of obscuration. Medical lore persisted, but it was corrupted with fanciful and puerile superstitions. Not until the Revival of Learning does any real advance begin to be made.

The history of botany from 1500 onward has been divided into four periods called respectively the Encyclopedic Period (1500–1650), the Systematic Period (1650–1800), the Morphological Period (1800–1890), and the Dynamic Period (1890–   ). The terms really seem to express successive ideals which have unconsciously animated the science and which, as we shall see, could only have developed in this special order.

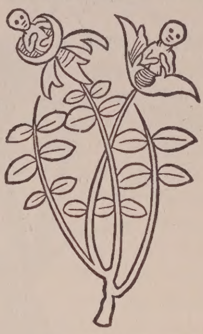
The studies we shall soon take up rest particularly upon the work of the second of these periods — the Systematic. We shall defer to a later time the detailed consideration of the work comprehended under the last two.

A. THE ENCYCLOPEDIC PERIOD

(1) *On the Continent.*

After the invention of printing in the middle of the fifteenth century, many works of considerable antiquity which had passed a long existence in manuscript were put into print. Among them were several works of a medical nature. Much curious matter is found in these old books. They were often embellished with woodcuts so crude that it is quite impossible to recognize the plant intended. One of these old herbals, or medical picture-books which gained great repute was the *Ortus sanitatis** or "Garden of Health," first printed by Jacob Meydenbach in 1491. It deals not only with plants but also with mammals, birds, fishes, and stones. It contains pictures of a unicorn, the "tree of paradise," and a "narcissus," with the Greek youth himself occupying the center of the flower (Fig. 73).

In 1530 a remarkable advance was made in plant iconography when there appeared in Strasbourg the *Herbarium vivæ eicones* of Otto Brunfels — the first of the so-called German Fathers of Botany.



"Narcissus" [Ortus Sanitatis, Mainz, 1491]

FIG. 73. — Woodcut of "Narcissus" [from *Ortus sanitatis* or "Garden of Health."

In this epoch-making work a series of very lifelike wood engravings formed the main theme (Fig. 74), and these were explained by quotations from ancient Greek and Roman writers on botany. No one seems to have suspected that the plants of Germany were not those which grew along the Mediterranean. The names of medicinal herbs had become much confused, and many German plants were sailing under Greek names which did not belong to them at all. Brunfels clears up a few of these errors, but makes gross blunders in regard to others, and really gave the world very little that was new. His ideal may be expressed best by quoting his own words: "In this whole work I have no other end in view than that of giving a prop to fallen botany; to bring back to life a science almost extinct. And because this has seemed to me to be in no other way possible than by thrusting aside all the old herbals, and publishing new and really lifelike engravings and along with them accurate descriptions extracted from ancient and trustworthy authors, I have attempted both; using the greatest care and pains that both should be faithfully done."

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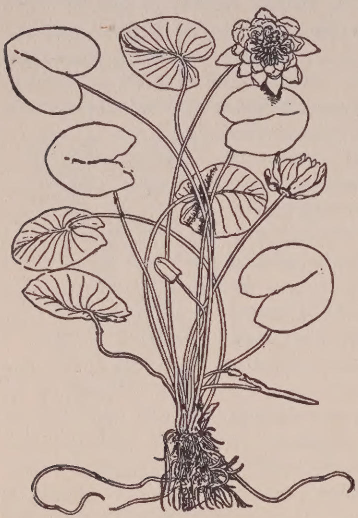
* See A. Arber, *Herbals* (1912), for an excellent discussion of these old books.

There is little attempt at classification in the book. Plants are divided into the herbaceous and the woody, and subdivisions are largely based on medical distinctions, for it must be remembered that botany was the science of the horticulturist and the physician.

Brunfels's work marks the beginning of an output of many such beautifully illustrated medical picture-books. Among other famous herbalists were the Germans Bock and Fuchs, the Dutchmen Doedens and L'Obel, and the Italians Mattioli and Colonna. In Switzerland worked Gesner and the Bauhin brothers, while Ruellius and d'Alechamps are outstanding men among French herbalists. The famous Flemish herbalist, Clusius, also takes high rank. Fuchs's herbal (Basle, 1542) is a masterpiece, and the wood engravings are "of extraordinary beauty." Among them are the first European figures of certain American plants such as the Indian corn and the pumpkin. Later herbalists helped themselves liberally to these figures, which ornament the "most beautiful herbal ever produced."



"Nenuphar" = *Nymphæa alba* L., White Waterlily [Brunfels, Herbarum vivæ eicones, Vol. I. 1530].

FIG. 74. — Woodcut of Water-lily from Brunfels's herbal (1530).

We have called the period of biology from 1500–1650 the Encyclopedic Period. It was a time of great activity; America had been discovered; Africa and the East were visited more and more, and into Europe poured a stream of new plants and animals. Botanical gardens were established for the culture of medicinal herbs. Thus there came to be an ever-increasing assemblage of plants, and naturally questions of identifications became more and more involved; the encyclopedic accumulation was becoming a chaos.

(2) *The Development of Botany in England.*

Before we explain how order gradually asserted itself, let us briefly review the development of botany in England. English botany has a particular interest for us, since it was the English who did the early work on the American flora and classified it in accordance with English principles.

Just as in Greece, English botany started with the medicine-men—in this case the Druids. These strange priests performed rites similar to those of the Grecian fraternity; for example, the mistletoe must be cut from the tree with a gold knife and received into a white ox-hide if its virtues were to be preserved; vervain must be dug with the left hand and always at the rising of the Dog-Star and in the absence of the sun and moon. Selago is to be gathered by a Druid clad in white and barefoot, and it must not be touched with the naked hand.

The Saxons brought a similar lore with them when they invaded England. Two Saxon manuscripts from about the tenth century have come down to us. One is the "Lacnunga" and the other the "Leech Book of Bald." Both are compilations or copies from far more ancient sources. As Rohde * says "It is almost overwhelming to recognize that possibly we have here fragments of the plant lore of our ancestors who lived when Attila's hordes were devastating Europe, and that in the charms and ceremonies connected with the plucking and administering of herbs we are carried back to forms of religion so ancient, that compared to it, the worship of Woden is modern." Through these pages move dim figures of trolls, moor-gangers, and "stalking fiends of the lonely places, creatures whose baleful eyes shone like flame through the mist." These old manuscripts are superficially Christian, for many are the directions for gathering herbs through the use of Christian rites. But underneath is a layer of Woden-worship, and still deeper lie traces of the mysterious archaic wisdom-religion once common to people all over the world.

The "Leech Book of Bald" was penned by one Cild about A.D. 900–950 and seems to have been the manual of a Saxon doctor. Traces of the medical lore of the Hindu "Atharva-Veda" can be detected in it. The "Lacnunga" is still older and describes among other things the war between Woden and the Serpent. This may be a version of the Babylonian myth concerning the battle of Bel with Tiamat. It is a charm against "flying venoms," those mysterious miasmas which caused disease, and it deals with nine sacred plants: mugwort, waybroad (plantain), stime (watercress), atterlothe (?), maythen (camomile), wergulu (nettle), crab-apple, chervil, and fennel. It runs thus:

* E. S. Rohde, *The Old English Herbals* (1922).

"These nine attack
against nine venoms.
A worm came creeping,
he tore asunder a man.
Then took Woden
nine magic twigs,
And then smote the serpent
that he in nine bits dispersed.
Now these nine herbs have power
against nine magic outcasts
against nine venoms
and against nine flying things
[and have might] against the loathed things
that over land rove.
Against the red venoms
against the white venom
[and so on for blue, yellow, green, dusky, brown, purple, venoms]
Against worm blast
[and so on for water, thorn, thistle, ice, venom, blasts]

If any venom come
flying from east
or any come from north
[or any from south]
or any from west
over mankind
I alone know a running river
And the nine serpents behold it
All weeds must
now to herbs give way,
Seas dissolve
[and] all salt water
when I this venom
from thee blow."

The potent "waybroad" (plantain) is further addressed in these words:

"And thou Waybroad,
Mother of worts,
Over thee carts creaked,
Over thee Queens rode,
Over thee brides bridaled,
Over thee bulls breathed,
All these thou withstoods't
Venom and vile things,
And all the loathly things,
That through the land rove."

The following concerns "betony the wort," another Saxon herb remedy: "It is produced in meadows and on clean downlands and in shady places. It is good whether for man's soul or for his body. It shields him against monstrous nocturnal visitors and against frightful visions." The roots of betony were gathered in August and powdered into a remedy which was good for sores, dim eyes, toothache, indigestion, nausea, snake-bite, and gout.

The period of the herbals was introduced from the Continent. In 1526 appeared the "Grete Herball," "which giveth purfyt knowledge and understandyng of all manner of Herbes and their gracyous vertues which God hath ordeyned for our prosperous welfare and helth, for they hele and cure all manner of dyseases and sekenesses that fall, or misfortune to all manner of creatoures of God created; practysed by many expert and wyse masters, as Avicenna and others," etc.

Two names stand out prominently among the English herbalists. These are William Turner and John Gerard. Turner, commonly called the Father of English Botany, was a clergyman and physician who lived in the time of Elizabeth. He traveled on the Continent and was a student of plants in the field. His "Herball" appeared in 1551; over 400 of the cuts in it were printed from Fuchs's blocks.

Gerard was also a physician, and, in what is now the very heart of London, established a private herb garden where he grew nearly 1,100 species of plants. He was in touch with collectors from all over the world, and even kings were interested in his garden. His herbal (1597) is an interesting work to the student of botany, containing as it does a picture of a barnacle-goose tree which produced birds and fishes on its branches, as well as a picture of "moss growing on a dead man's skull." Gerard's idea of classification may be illustrated by the way in which he devotes one part of his herbal to "trees, shrubs, fruit-bearing plants, rosins, gums, roses, heaths, mosses, mushrooms, and sea-plants."

The first man who really broke away from the dominance of medicine and described plants for themselves was Clusius or Charles L'Ecluse, the Belgian botanist (1526–1609). He knew about 4,000 plants and described them wholly apart from their value to man. His ideas of classification were, however, still rudimentary.

B. THE SYSTEMATIC PERIOD

As we have said, plants had now accumulated to such an extent that classification became imperative. We cannot stop to consider in detail the early attempts to bring order out of chaos. Both Clusius and the Englishman John Ray had recognized certain natural families of plants such as the umbellifers, grasses, and legumes, but not till 1700 did any noteworthy advance begin to be made, when Tournefort's *Institutiones rei herbariæ* appeared. In this work are described 10,416 species of plants, and though the main divisions are still trees, shrubs, and herbs, yet the minor categories are based on flower structure.

The one overshadowing name of the period is, however, that of the Swedish botanist, Linnæus or Karlvon Linné. This master systematist was born in 1707 and early manifested a passion for classification.

Linnæus cannot be said to have advanced the knowledge of plants very much, but he did a piece of work which had to be done and for which the botanical world must be eternally grateful — he set the Encyclopedic household in order. We should associate several important things with Linnæus.

1. He assembled and described in concise language the known species of plants; modern systematic botany goes back to the names given by Linnæus in his *Species plantarum* of 1753.

2. He definitely adopted a system of binomial nomenclature for plants. This is a system whereby each plant receives two names — that of genus and that of species. Binomials had been used more or less ever since the time of Theophrastus, but there was no consistent system, and some plants trailed long Latin sentences in place of names. For example, the following quotation from a letter of Dillenius to Linnæus shows clearly enough from what Linnæus delivered us.

"In your last letter of all, I find a plant gathered on the coast of Gothland, which you judge to be *Polygonum erectum angustifolium floribus candidis* of Mentzelius, and *Caryophyllum saxatilis foliis gramineis, umbellatis corymbis* of C. Bauhin; nor do I object. But it is by no means Tournefort's *Lychnis alpina linifolia multiflora perampla radice,* whose flowers are more scattered and leaves broader in the middle though narrower at the end."* Linnæus later called this plant, which worried his friend so much, by the name of *Gypsophila fastigata,* and so it is still called.

3. Finally, Linnæus put forward an artificial system of classification of plants based particularly on the number of stamens in the flower. It took the botanical world by storm; counting stamens became a favorite indoor pastime for ladies and hobbyists, and even to this late day botany has scarcely recovered from the reputation of being a trivial pastime. In justice to Linnæus it should be said that he cannot be held responsible for the silliness of some of his disciples. He set forth the artificial system as a temporary expedient, while he himself worked on a natural system which he never finished.

Natural systems of classification were progressively completed under the Jussieus (uncle and nephew), De Candolle, Endlicher, Bentham and Hooker, Braun, Eichler, and finally Engler and Prantl,

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* Quoted by Sargent in *Plants and Their Uses* (1912).

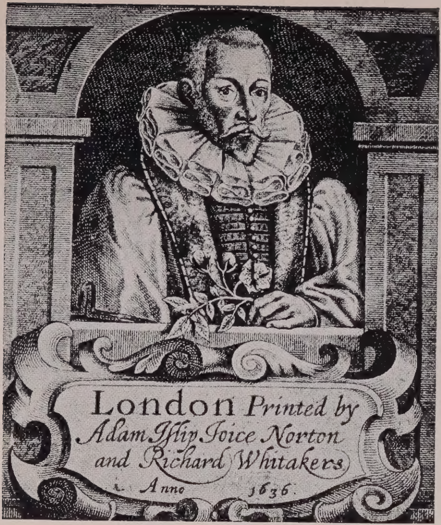
London Printed by
Adam Islip Joice Norton
and Richard Whitakers
Anno 1636.

FIG. 75. — John Gerard, a Famous English Herbalist (1545–1607).

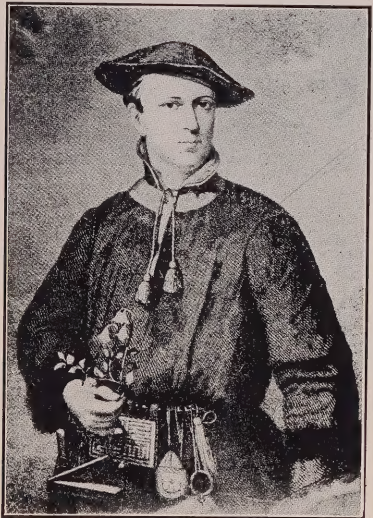

FIG. 76. — Karl von Linnæus, the Most Famous of Systematic Botanists (1707–1778).

whose system has been largely adopted by the civilized world. The work is by no means finished, since new discoveries constantly necessitate reorganization in our views of plant relationships. No further back than 1918, a system varying considerably from the Englerian so appealed to the writer that it has been adopted in his advanced courses as a better expression of the actual affinities of the great groups of plants.

C. THE MORPHOLOGICAL PERIOD

About the year 1800 the botanical stream began to be deflected into a new channel. Of course we do not mean that all workers abandoned the systematic field; it was rather that certain explorers entered a new country and their students followed them and made it known. The perfection of the microscope and the advance in technique were contributory causes, and Germany was the country where the new work in anatomy was actively carried on. It spread to other countries and, finally, from the painstaking investigations of minute organisms, as well as from laborious study into the minute structure of the higher plants and animals, came the magnificent induction which we call organic evolution. This idea was not new to the world; the Greeks and even the Egyptians and Hindus had speculated about the chain of life which ran from minerals to man; it was debated by scientists before Darwin, but the *Origin of Species* burst upon the general public like a thunder-clap and started reverberations whose mutter lingers even to our day. It is sufficient to say that no one qualified to judge of the matter has any shadow of doubt but that species have originated through an evolutionary process. It is, however, one thing to prove the fact of evolution and another to explain how and why it has taken place.

D. THE DYNAMIC PERIOD

About the year 1890 the center of interest began to shift to this very question — how and why do organisms evolve? Very naturally the answers must be sought in the fields of forces and energies — in other words, in the domain of physiology and ecology. To-day there has developed a school of biology which, through experiment in the application of physical forces to living matter, seeks the solution of the question. Much has been accomplished, but still we must confess almost total ignorance concerning the why and how of evolution.

Yet, after all, this is not particularly surprising. Scientific positivism, restricting its field of investigation to the sensible world, ought hardly to expect to solve the problem of causation. It is encouraging to see that the deeper thinkers in the ranks of science are beginning to recognize this elementary truth.

In this cursory review we have tried to show that the phases of botanical history succeeded one another in logical sequence. First economic considerations and the amassing of material; next, the sorting and classifying of the material; then, a more close and detailed study leading to the realization that plant and animal forms are related to one another like links in a great chain of being; and finally, a search into the world of physical causes for an explanation.

46. *Modern Principles of Classification*

We shall now turn our attention to systematic botany proper and study the basic principles which have been slowly worked out to guide the modern systematist in classifying plants.

A. THE MEANING OF THE TERM *SPECIES*

Every one is familiar with the fact that certain individual plants are closely related — we speak of them collectively as a certain kind of plant. White daisies, for example, vary a little in size, leaf shape, number of ray florets, etc., but they are all essentially one kind of plant. The same thing is true of the white pine, the red clover, the beech-tree, and so on for thousands of other cases. The botanist expresses this idea of intimate and fundamental sameness by saying that the individuals belong to a single species; the word being just the same in either its singular or its plural form.

Many attempts have been made to define the word *species*, but it is a difficult thing to do. The following are a few definitions which the writer has gathered:

> "There are as many species as God created in the beginning." — Linnæus. (To put this differently: A species is the special creation of God.)
>
> "A group of interbreeding individuals regarded by experts as having about the same degree of resemblance as parent and offspring." — Sargent.
>
> "A group of animals or plants, the members of which resemble one another so closely that to know one is to know all." — Parker and Haswell.
>
> "A group of interbreeding individuals, which, while they may differ markedly among themselves, yet resemble each other more closely than they do those of any other group; the characters that distinguish the group being considerable, not obliterated by intermediate forms, and inherited from generation to generation." — Hegner.
>
> "A species is a group of individuals that closely resemble one another owing to their descent from common ancestors, which have become more or less sharply separated from all other coexisting species by the disappearance of intermediate forms." — Dendy.

The reason why the term *species* cannot be rigidly limited is suggested by Dendy's definition. If forms come into existence by a process of evolution, we naturally expect that there are going to be transitions from one to another. If the botanist, then, has a complete series of forms before him, how can he say where one species begins and another leaves off? It is only when the hazards of evolution have destroyed connecting links that clear-cut "species" become recognizable.

Minor groups included within a species and connected by gradational forms with other members of the species are called *varieties*. They are commonly considered to be incipient species.

The species problem is further complicated by the well-known fact that species sometimes hybridize with one another and thus all sorts of perplexing blends may arise.

B. THE GENUS

All of us have noted that species, like individuals, are often closely related; thus there are red oaks, white oaks, scrub oaks, black oaks, and many others. The botanist recognizes this also and puts all the species of oaks together into the genus *Quercus*. The species just listed then become *Quercus rubra*, *Quercus alba*, *Quercus ilicifolia*, *Quercus velutina*. Leaf and acorn of six species of the genus *Quercus* are shown in Fig. 77. It should be noted that a species name is an adjective and that standing alone it means nothing — a *rubra* or an *alba* standing alone has no more significance than have the corresponding English terms, *red* or *white*. But when added to the *genus* name it carries a very definite meaning. The plural of the word *genus* is *genera*.

C. THE HIGHER GRADES OF CLASSIFICATION

Even as similar species are united into genera, so similar genera are united into families. Thus there are many genera of monocotyledonous plants whose flowers have three sepals, three colored petals, six stamens, and a superior gynœcium of three carpels. Such are *Trillium*, *Tulipa* (tulip), *Hyacinthus* (hyacinth), *Polygonatum* (Solomon's seal), *Erythronium* (dog-tooth violet), etc. These are all placed in the family *Liliaceæ*. Another group of monocotyledonous genera have the same structure as the last, except that the ovary is inferior; these are assigned to the family *Amaryllidaceæ*. Still others have the amaryllis structure, except for one point of difference — they possess not six stamens, but three; these make up the family *Iridaceæ*.

Furthermore, it becomes evident through study that the flowers of these three families — *Liliaceæ*, *Amaryllidaceæ*, *Iridaceæ* — are based on a plan of three, that they all have anatropous ovules, and that their endosperm is fleshy. These characters indicate real genetic

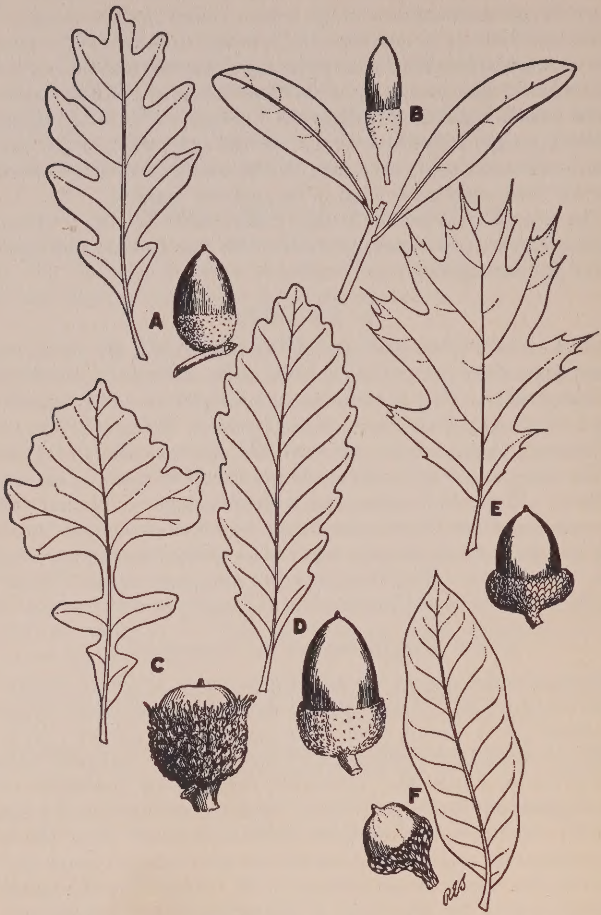

FIG. 77. — Leaf and Acorn of Six Species of the Genus *Quercus:* A, *Quercus alba* L.; B, *Quercus virginiana* Mill.; C, *Quercus macrocarpa* Michx.; D, *Quercus Prinus* L.; E, *Quercus rubra* L.; F, *Quercus imbricaria* Michx.

affinity, and consequently the three families with others of allied character are placed in the order *Liliales*.

As a result of similar studies it has been shown that the grass family (*Gramineæ*) and the sedge family (*Cyperaceæ*) are closely related to one another and make up another order called the *Graminales;* while the cannas (*Cannaceæ*), bananas (*Musaceæ*), gingers (*Zingiberaceæ*), etc., constitute the order *Scitaminales*.

All three of these orders agree with certain other ones in a single feature with which we are familiar — they all have monocotyledonous embryos. In addition to this, their leaves are usually parallel-veined and their flowers are usually based on a plan of three. They are all put into one great sub-class called the *Monocotyledoneæ* and this is merged with another sub-class, *Dicotyledoneæ*, into a single class *Angiospermæ*, which is characterized by having its seeds enclosed in ovaries. In contradistinction to the class *Angiospermæ* are the classes *Gymnospermæ* and *Aspermæ*. The *Gymnospermæ* bear their seeds on an open carpellary leaf, while the *Aspermæ* have no seeds at all. Finally all three of these classes are merged into one of the great divisions of the Plant Kingdom called the division *Embryophyta*, which means that its members all have an embryonic state in which they depend upon their mothers for their early support and nutrition.

Let us now review the procedure and classify our friend *Trillium erectum* through all the grades from top to bottom. Another case for comparison, that of the Christmas-fern, is placed beside it.

Division *Embryophyta*	Division *Embryophyta*
Class *Angiospermæ*	Class *Aspermæ*
Sub-class *Monocotyledoneæ*	Order *Filicales*
Order *Liliales*	Sub-order *Isosporineæ*
Family *Liliaceæ*	Family *Polypodiaceæ*
Genus *Trillium*	Genus *Polystichum*
species *erectum*	species *acrostichoides*

It will be observed that in the classification of the fern we used the term *sub-order*. Such intermediate groups between two others are permissible throughout the scheme. Thus a family may be divided into tribes, while a large genus is frequently split into sections.

It should also be noted that names of orders end in *-ales;* of families in *-aceæ;* the higher ranks of classification, however, have no formal endings.

D. THE VIENNA RULES AND THE PRINCIPLE OF PRIORITY

In order to establish an orderly and universal system of nomenclature, international botanical congresses are called from time to time. One of particular importance to students of the flowering plants was held in Vienna in 1905, when all questions relating to taxonomy were thoroughly discussed and the results were embodied in a set of so-called Vienna Rules which were voted upon and adopted by delegates from all the leading nations. These rather complicated rules relate to questions of priority, synonymy, citation of authorities, endings, etc.

As a starting-point for the nomenclature of the flowering plants, it was agreed to go back to the first edition of Linnæus's *Species plantarum* of 1753 and to take up no pre-Linnæan names, viz., names which would take priority over those used by Linnæus. It was also agreed that the validity of plant names given since Linnæus should also be based upon the rule of priority. Thus the name *Hydrangea arborescens* was given by Linnæus in 1753 to a certain plant. In 1803 Michaux in his *Flora boreali americana* called the same plant *Hydrangea vulgaris;* in 1816 Pursh gave it the name of *Hydrangea cordata.* Only one of these can stand, and that is the name given by Linnæus. The two others are called *synonyms.* Such synonyms often get into the horticultural trade, and it is almost impossible to displace them; hence, it comes about that some plants are known by several names. It should be borne in mind that only one of these is technically valid.

In order that a plant name should be complete, the name of the authority must be cited. In case the authority is a name well known to every one, abbreviation suffices. The common steeple-bush or hardhack is not simply *Spiræa tomentosa* but is *Spiræa tomentosa* L., the L standing for Linnæus. The strawberry is *Fragaria virginiana* Duchesne. This may seem absurd to the beginner, but it is the only way in which a strict maintenance of the priority rule can be assured, and it also makes us sure that we are dealing with the exact species which a certain author has named.

Now we come to a more complicated problem. Often in our manuals of botany we find names of two authorities appended to a plant name. Consider for example the name of our common hay-scented fern — *Dennstædtia punctilobula* (Michx.) Moore. In 1808 Michaux described this plant as *Nephrodium punctilobulum;* in 1857 Moore decided that it did not belong in the genus *Nephrodium* and transferred to the genus *Dennstædtia.* Hence the name became the one which we give above, viz., *Dennstædtia punctilobula* (Michx.) Moore. Both Michaux and Moore are partly responsible for the name. The species name applied by Michaux is valid no matter what happens later to the genus. If Moore had called the plant *Dennstædtia pilosiuscula,* his species name could not be retained to-day.

The above one or two elementary considerations show that the science of taxonomy is not simple. It demands fair play and a willingness to meet foreign scientists half-way and to make concessions if there is promise of ultimate stability. We are sorry to say that these principles have not always been observed in nomenclatorial disputes.

E. APPROPRIATE NAMES FOR PLANTS

A question sometimes asked by the layman is: Why do botanists use Latin names? The answer must be evident. Common names are almost as many as people who use them. Thus, *Equisetum hyemale* L. is variously called Dutch-rush, horsetail, scouring-rush, shave-grass, and scouring-reed.

But much more serious than this is the fact that the same common name is applied in different parts of the country to plants which have absolutely no relationship to one another. Consider the name "mayflower." In Indiana it is applied to *Podophyllum peltatum*, a member of the barberry family; in New England it means *Epigæa repens*, the trailing arbutus (heath family); in England it is applied to *Cratægus*, the hawthorne (rose family); also to *Caltha palustris*, the marsh-marigold (buttercup family); and to *Cardamine pratensis*, the cuckoo-flower (mustard family); in the West Indies it means *Amerimnon Brownei*, a member of the pea family. On the contrary, a plant has but one valid Latin name, and all cultured men everywhere are more or less familiar with the Latin tongue. To a Japanese, a Russian, a Turk, an Englishman, or a Frenchman, *Equisetum hyemale* L. means one definite species of plant and no other. We have already explained the reason for the use of Greek and Latin terminology in the sciences.

Now suppose one were to discover several new plants belonging to one genus and it became one's duty to devise a generic name for them — how would it be done?

The name might be a descriptive one based on some special peculiarity of the plant. Such are among the best types of names, since they enable one to remember it by associating it with a striking feature of the plant. Names based on this principle are *Helianthus*, *Hæmatoxylon*, *Brachyphyllum*, *Sarcophyte*, *Ichthyosoma*, etc., or, from the Latin, such as *Trifolium*, *Sempervivum*, *Gladiolus*. Most new generic names to-day, however, are taken from the Greek.

If the desire was to honor some one intimately connected with the discovery of the plant, a name formed like the following would be appropriate: *Oakesia*, *Dahlia*, *Jeffersonia*, *Brunfelsia*, *Dioscorea*, *Galenia*, *Linnæa*. In some cases a name taken from other languages is appropriate. *Tsuga* and *Ginkgo* are derived from the Japanese; *Araucaria* is derived from the language of a South American Indian tribe; *Tumboa* is a negro name; while *Camassia* is from the language of the North American Indian.

As to species names, these might be descriptions of color, habit, leaf-shape, etc. (for example, *rubra*, *alba*, *lanceolatum*, *pubescens*, *gigantea*, *bulbosus*, *macrocarpa*). They might again honor a friend connected in some way with the plant (*Braunii*, *Woodworthianum*, *Baileyi*, etc.); they could be derived from names of places (*canadense*, *nova-angleæ*, *californicum*), or from habitats (*aquatica*, *sylvaticum*, *montana*).

Since species names are adjectives, they must agree in gender and case with their genus names.

CHAPTER IX

GENERAL ECOLOGY

47. *Introduction*

We have finished the elementary study of the plant's body and have seen that many of its transformations of form have arisen in evolution as adaptations to various environments. We have learned somewhat of the language of systematic botany, so that we are able to identify plants through the use of the current manuals of plant determination. There remains one more broad field which enters naturally into the present phase of our work, since it is concerned with obvious aspects of plant life and does not require expensive or elaborate apparatus for its study. This is the subject of general ecology.

Ecology is one of the newer phases of botany. It will be recalled that the term comes from the words *oikos* = "house" and *logos* = "a discourse." Hence it is the science which treats of the plant "at home" in its relation to climate, to soils, and to other plants and animals. Each plant is, as it were, a point upon which the forces of the environment come to a focus, and the form which it assumes is the resultant of its hereditary factors modified and restricted by these forces. Therefore it follows that ecology is an aspect of the work of the newer dynamic period of biology. It is a composite or synthetic science which needs the help of all the sciences for its successful prosecution. The investigation of the inorganic factors of the environment is comprehended under meteorology, chemistry, and physics, while to understand the organic factors which are at work, one must needs know botany and zoölogy. Finally, to interpret the effect of all these forces upon the plant one needs a sound knowledge of plant anatomy and physiology.

How, then, shall one begin the study of ecology? It would seem logical to try to disentangle and to classify the complex of forces of the environment and to study their separate influences upon the plant. In actual practice this is a difficult thing to do. The influences of light and heat, for instance, are intimately related; again, the relative influence of soil texture as opposed to soil chemistry in producing a certain effect is often impossible to determine. But after this analysis has been in measure accomplished and after the influence of the separate factors has been partially determined, then the ecologist arrives at his main problem, which is the study of plant communities separated and distinguished from one another by some set of dominant ecological factors.

Ecology is a science still very young. It is loaded with a mass of detailed, catalogued observations which have never yet been properly interpreted; it is burdened with an unstable terminology, each worker tending to devise a set of barbarous terms for simple facts; and finally it suffers from dilettanteism. As a "new science" promising quick results and doctoral theses, it has too often attracted people not overly endowed with scientific training (or brains), and the results have been just what might have been anticipated.

48. *The Classification of Ecological Factors*

The factors at work upon the plant can be classified as physical and biotic. Under the former are included heat, light, wind, atmospheric humidity, soil wash, and the character of the substratum as to physical and chemical properties. The latter comprises such influences as are due to the activities of other plants or animals. Such are, for example, competitive crowding, the effects of bacterial, fungus, and insect parasites, the modifications induced by symbiosis, the work of earthworms, and the profound disturbances introduced by man. Much of this material will be discussed in other connections in later chapters of this book, but a cursory treatment will serve here to indicate the nature of the problems with which ecology deals.

A. THE INFLUENCE OF HEAT

The life of each plant ranges between two points of temperature. At the minimum temperature its activities can hardly take place because of cold; at the maximum the same inhibition occurs because of heat. Between the two lies a certain optimum temperature at which it flourishes best. These points vary widely for different plants. There is no degree of cold sufficient to destroy plant life altogether. Certain arctic algæ can grow at a temperature only a little above 0° C. (32° F.). They can be frozen in snow and blow like dust about the Polar lands without harm. Certain bacteria can even survive the temperature of liquid air (−190° C.).

Furthermore, in spite of common opinion, there seems to be no plant which has any device to protect it against cold. As we learned when studying the horse-chestnut twig, all the protective scales and woolly wrappings are instituted to keep down evaporation of water during the winter drought. The seeming delicate chickweed (*Stellaria media*) often freezes solid in winter and becomes as brittle as glass, yet a few warm days in spring suffice to restore it to vigorous growth. Warming tells of a seaside plant (*Cochlearia*) on the arctic shore of Siberia which endured a winter temperature of −46° C. accompanied by biting polar winds; yet the following spring it continued its flowering, which had been interrupted by the winter. On the other hand many of our warm-weather garden plants blacken and die with the first light frost. Hardiness or its lack, then, is a property of the living substance itself.

The vegetative activities of temperate land plants begin at about 6° C. (43° F.), though tropical plants require from 10° – 12° C. for the same awakening. Wheat, a cold-climate plant, will germinate on a block of ice, and the heat it releases will melt a hole for its root; the castor-bean, on the contrary, a native of the tropics, requires a high temperature if it is to be germinated successfully. As to the upper or maximum limits, most plants can stand about 45–50° C. but there are certain algæ which can grow in hot springs where the water is at the temperature of 80° to 90° C. Seeds or spores are often extremely resistant to heat. It is well known that the spores of bacteria can resist the temperature of boiling water if it is not too prolonged; they can even stand 180° C. for a short time.

It is interesting to learn that the optimum temperature for vegetative and reproductive activities is not always the same. The nut-grass or chufa (*Cyperus esculentus*) ranges from the Southern United States up to Maine, but it has never been found fruiting in the northern part of its range, where it reproduces entirely by tubers. *Sagittaria graminea*, one of the arrow-heads, runs from the Gulf of Mexico to Hudson Bay. It fruits up to Long Island Sound, but north of that it depends, like the nut-grass, on its tubers for reproduction. On the other hand, some temperate land plants taken to the tropics "run to leaves"; this means that they can raise the vegetative temperature point, but not the reproductive. Some plants, however, can raise or lower both points, and this permits them to have an extensive range. Thus the apple produces good fruit from Quebec to Mexico and from Scandinavia to Greece.

Temperature and the amount of heat available during the growing season largely controls the north-south areal distribution of plants as well as its vertical distribution from lowland to mountain. It was upon this basis that Merriam established the North American life zones. Each zone is marked off by biotherms, viz., the total amount of heat above 6° C. (43° F.) which is available for growth between spring and fall. Upon this basis the North American continent can be divided into three great belts or transcontinental regions which are called respectively the Boreal, covering the lands from the Polar sea southward to near the northern boundary of the United States, and running still farther southward along the mountain ranges of the east and west; the Austral (*auster* = "south wind"), which takes in the whole of the United States and Mexico with the exception of the mountains and the hot lowlands of southern Florida; and finally the Tropical, which touches a small part of Florida and includes the lowlands of Mexico and most of Central America. These regions are divided into narrower zones based upon their characteristic flora and fauna. Finally the zones are divided into areas bounded by meridians of longitude and following one another from east to west across the continent. The areas are based upon the relative amounts of rainfall.

B. THE INFLUENCE OF LIGHT

Strong light induces a stocky growth; on the contrary weak light tends to elongate the internodes and to draw the plant out into a slender form. Any gardener is well aware of the deleterious effect of shading on plants that normally grow in full sunlight. On the other hand, there are certain shade-tolerant or shade-loving plants. They are usually large-leaved with their blades expanded to catch all the available light, and often organized into leaf-mosaics. The effect of abnormal shading upon a plant normally adapted to full sunlight, is manifested in both its form and structure. The leaves, in particular become weaker and more filmy, and the air spaces in them are enlarged. Sun plants, on the contrary, are often wrapped in wool or coated with wax and the epidermal layer is thickened.

The factors introduced by heat and dryness are difficult to distinguish from those due to intense light. It has recently been pointed out that the amount of light available each day has a remarkable effect upon plant development, particularly in connection with reproduction. If the hours of daylight be shortened, the plant proceeds to flower and fruit right away, whereas with longer periods of daylight they remain in the vegetative state. Thus a species of wild aster may flower in August in Vermont and delay till November at St. Louis. Gardeners have even learned that varieties of autumn chrysanthemums stated by Vermont nurserymen to flower in September will delay till mid-October in Massachusetts.

This response to length of day works to the great advantage of northern plants; it permits the Esquimaux on the shores of Hudson Bay to raise a potato crop in a short summer of five or six weeks.

C. WIND AND ATMOSPHERIC HUMIDITY

Wind and atmospheric humidity have a great effect upon the rate of water loss from the plant. American gardens, for instance, are far inferior in beauty to those of England, where the saturated air from the encompassing ocean provides ideal conditions for plant growth. Strong winds exert a deforming effect upon plants; one need only observe the trees of wind-swept coasts and headlands to realize the deforming power of the sea gales. It is commonly believed that the lack of trees on the prairies is due to the winds, which dry out the soil to such a degree that tree seedlings cannot establish their root systems.

D. THE INFLUENCE OF SOILS

The soil factor plays a most important rôle in plant life, and the subject of soils has developed a whole composite science of its own, which includes mineralogy and petrography, chemistry, physics, and bacteriology.

E. HYDROPHYTES, MESOPHYTES, AND XEROPHYTES

The response of the plant to the water content of the soil is immediate and direct; in fact, water is generally held to be the greatest single factor in determining plant distribution. Based upon their relative water requirements we can divide plants into hydrophytes, mesophytes, and xerophytes.

The *hydrophyte* may live wholly immersed in the water, or only its roots and lower parts may be submerged. To the former category belong the marine seaweeds and the various pond scums, the hornwort (*Ceratophyllum*), the river-weeds (*Potamogeton*), etc. Many of these plants take their food salts directly from the surrounding water. To the latter group belong the numerous aquatic angiosperms which root in the soil at the bottom of the pond but throw their leaves and flowers into the air. Such are arrow-heads, pickerel-weed, and cattails. Water plants tend to reduce their woody tissues and to depend upon the buoyant power of the surrounding medium for their support; their submersed leaves are often delicate and are sometimes split up into capillary divisions even as are the gills of a fish, and presumably for the same purpose. They have no protective cuticle, and in consequence they dry out quickly when removed from the water.

Quite commonly the aquatic angiosperms are rhizomatous. Our northern hydrophytes withdraw their vital forces into the mud while the ponds are frozen. They often bear reproductive devices which are peculiarly adapted to water transportation or to overwintering.

The higher water plants all had immediate land ancestors; they have returned to a habitat which their far-off algal ancestors abandoned millions of years ago. Mrs. Arber * writes:

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* Agnes Arber, *Water Plants* (Cambridge, 1920).

"There is good reason to assume that the angiosperms were originally a terrestrial group and hence that the aquatic flowering plants existing at the present day can trace their pedigree to terrestrial ancestors. If this be the case, we may interpret the various gradations existing within the hyprophytic group, as illustrating a series of stages leading from ordinary terrestrial life to the completest adoption of an aquatic career."

The growth of hydrophytes around a body of water often exhibits an interesting phenomenon called *zonation.* In the deeper water will be found the submersed species such as water-lilies, or the water-buttercups with floating leaves. In the shallower water nearer shore a zone of arrow-head or water-plantain or pickerel-weed may appear; this may, in its turn, be followed by a marsh zone occupied by cattails and sedges, till finally one comes to the drier soil of the banks occupied by plants which will not tolerate so much water about their roots. So there may appear about a pond a number of sharply marked concentric zones of vegetation.

The rank and file of land plants adapted to ordinary soils are called *mesophytes.* Water is present in sufficient amount to supply normal vegetative activities, but it does not saturate the soil.

Xerophytes are plants of soils so dry that the optimum amount of water is lacking. They constitute one of the most peculiar of ecological groups of plants. Their bodies are modified not only to retain water but to minimize its escape. The cacti are xerophytes *par excellence.* Fleshy bodies, often heavily cuticularized and provided with thorns, sunken water-pores, hairy coverings, and reduced leaves are all characteristic xerophytic modifications. Such plants are often provided, too, with deep-lying, subterranean members adapted to the storage of food and water.

F. ECOLOGICAL GROUPS BASED UPON SOIL TYPES

The composition of the soil, physical and chemical, exerts a profound effect upon plants. Temperature, porosity, permeability, texture, humus-content, and the presence or absence of soil organisms all play their parts. Of particular moment to this brief treatment is the influence of dominant chemical compounds in controlling the distribution of vegetation. The influence of an excess of lime or of acid, or of sodium chloride or nitrogen, is particularly marked. This is the basis for a common ecological classification of plants into *calciphiles,* which prefer a limy soil, and *calcifuges,* which avoid it. Those which grow best in acid soil such, for example, as the rhododendrons and many other ericaceous plants, are termed *oxylophytes.* Plants of the salt-marsh, which will tolerate considerable quantities of sodium chloride and other sea salts, are called *halophytes,* while those that grow best in rich nitrogenous soils are known as *nitrophytes.*

Other technical terms have been coined in great diversity to apply to plants which inhabit various other soil types. Thus the *psammophytes* grow in siliceous sands; *lithophytes* live on rocks; and *helophytes* prefer the marshes. The etymology of these words is usually sufficient to make their meaning clear.

G. BIOTIC FACTORS

The biotic factors are the living forces of the environment. Earthworms play a prominent part in loosening or comminuting the soil and in facilitating the penetration of air; bacteria bring about the formation of humus and render the necessary nitrates available. Above ground the plant is subjected to the attacks of leaf-eating or boring insects, of destructive fungus parasites, of grazing animals, of competition with its fellows, and above all to the modifications which man introduces into its environment. The forest retreats to make way for his culture crops, and as the hot sunlight reaches the forest floor the delicate humus plants succumb and their place is taken by a host of hardy and often pestilent European weeds whose seeds find facilities for migration never before available.

Building, manufacturing, and mining operations introduce profound changes into the balance of Nature, while in the train of commerce many fungus and insect parasites are introduced to work havoc among a native vegetation never adapted to withstand them. In this connection it is of interest to note that the native American vegetation is less vigorous than the European. It seems to belong to an older evolution, and it is particularly worthy of remark that our Atlantic coastal plants are very closely allied to those of Eastern Asia.

Very few American plants have shown a tendency to become weeds in this or in other countries. A few exceptions are our cacti and some of our composites; but on the other hand, European forms have invaded America like a conquering army and have become our most pestilent weeds, gradually driving the native flora before their advance. The dandelion, plantains, chickweeds, pigweeds, white daisy, sorrels, and docks are all European plants. It may be noted in this connection that the European animals also tend to drive out our native fauna: the rat, English sparrow, and starling, hardy vagabonds from the Old World, have more than held their own in competition with the native rodents and birds.

49. *Plant Communities*

We come now to what is perhaps the central and most interesting of the phases of ecology, viz., the subject of the communal life of plants. In taxonomy and classification the unit of study is the individual species, but in ecology it is the plant community — an assembly of several or many species of plants living together in a meadow, a salt-marsh, a desert, or whatever may be.

No organism lives to itself alone. Each exists in a state of extremely unstable tension. A modification of one force brings about the readjustment of the whole social system of which it is a part. A summer drought, for example, may kill certain of the more shallow-rooted plants; immediately their bodies are seized upon by a micro-flora of bacteria and fungi and are reduced to humus. Thereby the physical and chemical conditions of the soil are altered and the neighboring plants are affected. At the same time the removal of these plants permits the penetration of more light into the "household." In response, the surrounding plants alter their shapes and for a short time are able to grow more vigorously. But gradually they enter into competition once more, and the state of tension reasserts itself. Under the utmost of favorable conditions any species would, as we have learned, cover the earth in short order, but with this ceaseless warfare against the forces of the inorganic and organic environment, a sort of armed truce is established which is broken at the least opportunity. Life forever presses against its boundaries.

A. THE PLANT FORMATION

All the ecological factors which we have mentioned are brought to bear upon the plant world, but it is evident that they are never all concentrated with equal intensity at the same point. The desert has its combination of dry soil, dry air, fierce light, and heat; the salt-marsh or the mountain-top offers another set of factors. Each combination sets a definite and peculiar stamp upon the plants which are subject to it and leads to a heterogeneity of flora over the earth. The vegetation is thereby broken up into ecological groups which are called *plant formations*. It does not matter particularly what the constituent species may be. In the American deserts cacti, yuccas, and agaves are the characteristic plants; in Africa the euphorbias and aloes assume similar shapes and play a similar rôle. In the northern hemisphere the *Ericaceæ* are typical plants of moorland formations; in Australia it is the *Epacridaceæ* which dominate such places. So the formation is an expression of certain defined conditions of life and is not concerned with floristic differences.

B. THE PLANT ASSOCIATION

Even as the great areas of vegetation can be divided into formations, so the formation itself is not homogeneous but can be subdivided into minor groupings of plants which are associated with slight differences of soil and water, and which take the name of *associations*. They may consist of one or of several species. In the Alleghenian woodland, for instance, there may be seen at one place associations of pines, at another associations of white birches with alders, or at a third mountain laurels and hemlocks. In the aquatic formation one place will show associations of water-plantain (*Alisma Plantago-aquatica*) with arrow-head (*Sagittaria*), another an association of cat-tail (*Typha*) and *Scirpus validus*.

Broadly speaking, we may classify formations into the two groups of *climatic* and *edaphic* — in other words, those which rest upon differences in climate, and those which are based upon differences in the soil where the plants grow. The formation introduced and controlled by man is sometimes set apart as a culture formation.

C. CLIMATIC FORMATIONS

The term *climate* means the average weather condition of a region as regards its temperature, moisture, and prevailing winds. One thinks right away of deserts, prairies, woodlands, of arctic and tropical lands, where the weather conditions impress a certain character upon the flora over broad areas, though differences in soil introduce minor edaphic modifications.

(1) *The Desert Formation.*

The desert formation is found wherever rainfall is scanty and irregular, while both the diurnal and the annual temperatures are subject to great extremes. The air is clear and dry. The soil varies widely in such places. Sometimes it is sandy and light and is heaped up into dunes by the wind; sometimes it is covered with flints or pebbles. There is no humus in the soil. After the slender rains the water evaporates from the shallow rain-pools and often leaves a deposit of white salt over the baked, mud-cracked soil. Rare oases and springy places occur where a more luxuriant vegetation manages to establish itself.

There is never enough water in the desert to support a close formation. Instead the plants are scattered here and there, with patches of bare sand between them. In the Colorado desert, for example, the spicy, gray sage-brush (*Artemisia*), and the greasewood (*Sarcobatus*) scantily clothe the sands. The vegetation is adapted to withstand long sieges of drought and heat. Some forms spend most of their life in the seed condition, or underground in the form of bulbs or tubers or rhizomes. Their development when the rains come is astonishingly rapid. In a few weeks they have thrown out their often brilliantly colored flowers, have set seed, and have again retreated from view.

Other forms stand erect, defying the trying climate as best they can. The tumble-weed habit is a common method of desert distribution.

Hardy * says of the Arizona desert:

> "Nowhere in the world is there such a combination of weird, ungainly, menacing shapes: giant candelabra cerei of most diverse varieties, mamillarias, opuntias, yuccas, agaves, dasilyrions, nolinas, creosote bush (*Larrea*) . . . and the formidable spines of several thorn bushes belonging to the acacia and mimosa type."

(2) *The Prairie Formation.*

The prairie is another characteristic American formation. The climatic conditions are severe due to the distance from the ameliorating influence of the sea. The summers are hot, dry winds sweep violently across the country, and the summer rainfall is but slight. The winters are long and severe, and there is an abundant snowfall.

Here grow numerous harsh, tufted grasses mixed with composites, legumes, and other herbs. Trees are mostly lacking except along stream banks or where planted by man. It is generally believed that the treeless state of the prairies is the outcome of special climatic conditions. At the time when the tree seedlings try to strike root, the surface soil is so dried out by the winds that they are unable to establish themselves. That trees grow well when introduced by man attests the truth of this opinion.

(3) *The Mesophytic Forest.*

In temperate climates, where moisture is sufficient to supply the needs of mesophytic plants, the forest is the characteristic formation. It is notable for its carpet of early tropophytes and for its mixed vegetation of dozens of both evergreen and deciduous tree species. Moisture is usually sufficient for all needs, and the plants are well adapted to withstand the rigors of the northern winter.

(4) *The Arctic Formation.*

The arctic formation is another of considerable interest. Vast areas of land bordering the Polar sea, both in America and in Eurasia, are covered with it. As one advances northward, the trees of the mesophytic forests gradually give way, till finally only a few tortured poplars, birches, willows, and the like remain. They dwindle in stature till they often become prostrate and trail among the moss hummocks, rising only a few inches into the air. Even the taller species show the effect of the rigorous climate. In Greenland, for example, the willow bushes, which grow two or three feet high, are densely branched and look as though they had been artificially sheared at their tops. This is due to the fact that the tips of the twigs which rise above the winter snows are killed, and hence a sort of natural pruning is effected.

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* W. E. Hardy, *The Geography of Plants* (Oxford, 1920).

The soil of the tundra region is always frozen beneath, but in summer it thaws out above, and the country becomes a maze of mud-holes. The streams, fed with snow water, eat out gullies, and the islands between them become moss- and lichen-covered tussocks where grow various hardy, acidophilic sedges, junci, and grasses, along with a few herbaceous dicotyledons. Dwarf birches, willows, and various shrubby, ericaceous plants cling to the drier hummocks. In more favored places such as southern slopes and stream banks one finds the local "arctic meadows." These favored spots become free of snow first in spring, and a considerable vegetation develops in the rich, black, moor earth. It is comprised mostly of angiosperms with brilliant flowers, such as dandelions, chickweeds, veronicas, saxifrages, bluebells, potentillas, fireweeds, and buttercups. Even the grasses take on colors and glitter with metallic violets, reds, and browns.

Rain and fog are almost constant phenomena, and the country is one of great monotony and desolation. In the bog-holes breed swarms of mosquitos. Insect life is so abundant in the Polar regions that they become the feeding grounds for innumerable migratory birds.

(5) *The Alpine Formation.*

The characters of the Alpine formation are rather similar to those of the far north. The term is applied to plant communities of mountains such as Mount Washington and the Adirondacks and Green Mountains. The physical conditions and the flora often simulate those of Polar regions. Differences in soil composition lead to edaphic sub-formations in the Alpine area, but in general the climatic conditions are similar for all. During the daytime the ground becomes hot, but at night there is correlative radiation of heat so that the air and soil become very cold. Toward sunrise a mist gathers and hangs over the mountain; the vegetation is soaked and the trees drip with moisture. This holds till about ten o'clock, when once more the intense light breaks through the mists and the earth is heated up again. During the day sudden snow-squalls are frequent, while hail-storms and rain assault the vegetation. It would seem that plant life under such extreme conditions must be of a peculiar type, and we find such to be the case. Rigid, wiry grasses and sedges with acid-loving heath plants border the bogs and ponds, where stunted spruces may also develop; on the dryer, rocky areas grow many xerophytic plants such as *Ledum groenlandicum*, a plant with leathery leaves, the lower surfaces of which are covered with wool. Pincushion-like domes of *Diapensia* or of *Arenaria* hug the soil; dwarf willows such as *Salix Uva-ursi* creep through the mosses, and while they rise barely three inches above the soil, may spread over an area a yard or more broad and be fifty to seventy-five years old. As one approaches the timber-line, the taller shrubs dwindle in stature and become gnarled and contorted into fantastic forms, constituting what the Germans have called *Krummholz*.

D. EDAPHIC FORMATIONS

Turning to the edaphic formations — those which depend upon local conditions of the substratum — one may mention a few common examples such as those of rocks, of the sand-dune, the sea strand, the swamp, and the moor.

A formation may be regarded as a loosely coherent organism, and it will serve to bring out this organic character if we treat a few of the edaphic formations from the standpoint of their ontogeny.

Every formation is born; it develops to its maturity (called the *climax formation*), and it must eventually pass away. The formation is initiated when an area of soil becomes exposed to colonization. It may be a fresh soil area laid down at the mouth of a river or heaped up by a glacier, or it may be an area denuded of its former vegetation through the action of running water, wind erosion, landslide, drought, fire, or some other factor. Into these bare areas the spores, seeds, and fruits of plants are carried by the various dispersive agencies. This constitutes the process of invasion through which the formation comes to birth. Then begins the struggle for existence, which becomes more and more tense as time goes on and new immigrants seek to enter. Finally a condition of stability is attained, but, as has been already pointed out, it is a stability which rests upon an equilibrium of contending forces and is easily upset. The state of stability constitutes the climax formation. In New England it is the mesophytic forest; on the stabilized sand-dune of the coast, it is the forest of pitch-pine; farther west, it is the grassland. The death or transformation of the climax formation is brought about by major changes in climate and by various catastrophes which destroy the plants.

(1) *The History of the Rock-forest Formation.*

The rock-forest formation is one of the most basic and fundamental types. In its microcosm one can witness in a general way the recapitulation of the story of the conquest of the land by vegetation. For, if our reading of the geological record be correct, there was a time when the earth itself was but a rocky mass destitute of plant life.

On the bare rock the formation is initiated by the very lowliest forms of crustose lichens, which absorb their necessary moisture from the small amount which clings to the rock after rain, and obtain their mineral salts by slightly dissolving away the mineral substances. As the years pass, fragments of them die and form a substratum of moist humus in which the higher foliose lichens and mosses can gain a foothold; these slowly add their dead debris to the mass. This tends particularly to accumulate in crevices, where more moisture is naturally available. Now the herbaceous seed plants appear, most of them being wiry grasses or other crevice plants, and finally a turf is established in which low bushes gain a foothold, to be followed in their turn by tree seedlings. After the grass stage, competition becomes active. Slowly the forces of weathering and of invading tree-roots break the upper layers of the rock into coarse gravel, and at last a dominant tree type reigns supreme, the climax formation having been attained. The rock-forest series is a common one in New England, and almost any mountainside will show it in all its stages.

(2) *The River-forest Formation.*

Another common series is that of the river sand-bar or flood-plain, which, if it reaches maturity, comes to its climax in the forest of hardwood trees. Very commonly, however, it never reaches the climax condition but is destroyed by high water during some of its earlier stages.

In the Connecticut River, for example, the retreating waters of the spring flood expose long sand-bars, which, as summer advances, exhibit an open formation of sand-loving annual weeds (psammophytes) such as ragweed (*Ambrosia*), cockle-bur (*Xanthium*), and beggar-ticks (*Bidens*). Since the bar is usually flooded in the spring, only annuals can gain a footing on its lower reaches. On the higher levels, however, various sand-loving grasses begin to appear, to be followed later as humus accumulates, by blueberries and myricas, willows, and cottonwoods, and finally by a climax formation of hardwood trees. This series is rather common, too, on the flood-plains of the rich river lands of Pennsylvania and Ohio.

(3) *The Lake-prairie Formation.*

The lake-prairie series presents us with another set of events. Every lake is a temporary phenomenon, since the entering streams dump their loads of sediment along its shores and bring about a progressive shallowing, while the outlet is gradually cut down so that its waters are eventually drained away.

The original lake bears its flora of water-lilies and other floating and submersed hydrophytes. The phenomenon of zonation is often marked along the shores. As it becomes shallower, the zone of shore vegetation begins to close in. The bog-moss (*Sphagnum*) appears and establishes a peaty substratum across which the cat-tails, sedges, and grasses begin their forward march. A time soon comes when only a peat-bog remains, and finally the prairie rolls over the spot.

In New England the grass and sedge stage is usually followed by a growth of alder (*Alnus incana*) or gray birch (*Betula populifolia*) or willow, and this gives way to the typical mesophytic forest of maples, oaks, hickories, birches, and other hardwoods.

(4) *The Mud-flat and Salt-marsh Formation.*

Characteristic of the Atlantic Coast are the mud-flats and salt-marshes which border the estuaries where the streams enter, and which, in the mud-flat stage, are submerged twice daily by tidal waters. The slimy salt mud is a difficult substratum for plants to colonize, and on the New England coast only two extreme halophytes play any prominent part in the process. These are the salt-water eel-grass (*Zostera marina*) and a true grass, *Spartina glabra*. As the soil builds up, there appears the narrow-leaved cat-tail (*Typha angustifolia*) along with various sedges and rushes; as it grows still firmer, certain grasses such as *Spartina patens*, *Distichlis spicata*, and *Puccinellia maritima* combine with the "black grass" (*Juncus Gerardi*) to form a spongy turf interspersed with "salt pans" where grow the sea-lavender (*Statice*), the seaside goldenrod (*Solidago sempervirens*), and the samphire (*Salicornia*). So long as the sea-water soaks the peaty soil, this is the climax formation.

Salt-marsh halophytes very generally exhibit xerophytic features. Water is abundant enough, but it is so heavily charged with electrolytes that its osmotic passage into the roots is inhibited and the plants are actually suffering for lack of water. As in the case of the Ancient Mariner, it is:

> "Water, water everywhere, nor any drop to drink."

As a consequence of this physiological drought the plants tend to develop fleshy, water-storage stems and leaves and to cover their bodies with thick epidermis and cuticle.

(5) *The Sand-dune Formation.*

We may consider one more example and one of the most interesting — that of the sand-dune. Shifting sand, too, is a difficult substratum for plants to establish themselves upon, and yet a few have adapted themselves to it, though they never succeed in establishing a close formation while the dune is in its young stages. Prominent on our

Atlantic coastal dunes and on those of the Great Lakes is the sand-grass, *Ammophila arenaria*, whose cord-like rhizomes burrow into the sand and whose stems creep upward as they become buried below. As the dunes become stabilized through the increasing cover of vegetation, other sand-loving herbs and shrubs begin to appear; such are the pinweeds (*Lechea*), wormwoods (*Artemisia*), crowberry (*Empetrum*), and *Hudsonias*. These convert the "white dune" into the "gray dune," and the gray dune in its turn gives way to the dune thicket of wild roses, sand-plums, sweet-fern, and poison-ivy. The dominant type which finally succeeds along the Atlantic Coast is the pitch-pine (*Pinus rigida*).

The white dune is a very unstable factor and is always traveling before the wind and migrating from place to place. It may encroach upon an inland forest and destroy all the trees, leaving a graveyard of dry skeletons as it moves away. In Asia Minor shifting sands are known to have buried the remains of ancient civilizations, from which they sometimes creep away to leave the ruins exposed.

50. *Conclusion*

If you have thoroughly assimilated the matter contained in the foregoing pages, you are in a position to observe Nature intelligently and to learn from her. You know that the plant world is one of intense, though silent, activity. Each spring a million seeds germinate in field and wood, but "some fell by the way side, and the fowls came and devoured them up: Some fell upon stony places, where they had not much earth: and forthwith they sprung up, because they had no deepness of earth: and when the sun was up, they were scorched; and because they had no root, they withered away. And some fell among thorns; and the thorns sprung up, and choked them: But others fell into good ground, and brought forth fruit . . . ."

This quotation taken literally is excellent ecology. It shows that the speaker had recognized the principle of the "struggle for existence" which is the keystone of Darwinism.

It should be emphasized that in the preceding studies we have merely used our eyes and fingers and the brains with which the good Lord provided us, to become familiar with matters that have stared us in the face all our lives and which we never saw before.

We have reached backward and have tried to assemble the scattered facts about plants which many of us have been storing up since childhood. We have tried to weave them into an organized body of knowledge by introducing such new material as was needed to make a consistent story. At the same time, however, the book has repeatedly sounded a new note and one which some students may have found bewildering. Perhaps it can be interpreted in this fashion. The schoolboy deals with *things;* his concern is with the perceptual world and with such simple concepts as may generally lead to immediate application — the building and direction of machines, the winning of games; in a word, to the conquest of the physical world.

The truly educated man, on the contrary, desires to look beneath the surface of things into the realm of *meanings.* He studies the linkages between seemingly unallied facts; he seeks for inclusive generalizations; he tries to build up within himself a realm of organized ideas. His method of approach to the world is synthetic rather than analytic. It does not necessarily involve the acquisition of myriads of new facts, though generally speaking the broader the factual base the more firmly will he build. Since, however, the world is a unity, its organization is reflected in its simplest parts. Common things are common only to common people. Sunflowers and pine-trees and salt-marshes are astounding phenomena, "and a mouse is miracle enough to stagger a million infidels."

The beginner in college stands at the place of transition between these two kinds of knowledge, the knowledge of things and the knowledge of meanings. I have tried not only to conserve the values of the past but to sound the note of the future. The new aspect of things comes slowly, but come it will if we do our part, always trying to understand.

PART II

THE ANATOMY AND PHYSIOLOGY OF SEED PLANTS

"If we took the trouble to call Nature into the witness-box, we should find that everything which is perceptible to the ordinary sight, has something even more important than itself hidden within it; the microscope has opened a world to us, but within those encasements which the microscope reveals lies a mystery which no machinery can probe."

Light on the Path.

INTRODUCTION

The preceding chapters of this book deal with the everyday world of plant life which lies open to all men's observation. With the simplest of instruments we have studied seeds, roots, stems, leaves, flowers, and fruits. We have seen that living things are in process of perpetual transformation and that the doctrine of evolution, far from being an obscure subject for academic speculation, is supported by evidence upon every hand if we will divest ourselves of prejudice and misconception and open our eyes to see.

We realize, too, that the evolutionary transformations are designed to adapt the plant to the environment and to provide it with every chance to triumph in the struggle for life. Only by the conquest of resistance does life go forward.

We have amassed a considerable botanical vocabulary and are able to identify the plants which grow in woods and fields and to describe them to others without danger of misunderstanding.

Finally, we have begun to realize, perhaps, that the bare scientific description of the world is a poor dead thing at best, and that our interest and enthusiasm are awakened when we begin to detect the body of universal principles which shines through "the living garment of Deity."

But we are college students able to deal with a subtler range of facts than those which are open to the layman's observation and which are set forth in Part I. In the coming pages, with the help of optical instruments, we enter a world of perception which is forever closed to unaided vision. Starting with a consideration of the units of living matter out of which bodies of plants and animals are builded, we shall advance to a study of the tissues and organs of the plant till finally, with the machine assembled, we shall be prepared to understand how it feeds, grows, and reproduces itself. So to the student who masters the factual knowledge included in this book and who intends his mind upon it, there will come the vision of a living organism evolving through the ages in a logical manner toward an exquisitely balanced efficiency and simplicity, and one into whose body is integrated many millions of years of historical experience.

Again and again the identical principles of structure and function brought out in Part I will be seen working in the finer worlds of cells, tissues, and organs. The anatomical elements of the plant's body are themselves entities of minor degree, and in each minor system are reflected the laws of the whole cosmos. Thus the cells, tissues, and organs have their racial and individual histories; they are associated in hierarchies; they exhibit profound division of labor. It is this deeper sort of knowledge which we seek, for in the last analysis life offers us but one problem and that is the problem of human evolution. We seek to learn the basic laws of the universe, not that we may exploit them to the gratification of our physical, emotional, or mental desires, but that we may conform our lives to their rule and build our house upon the rock.

CHAPTER X

THE STRUCTURE OF THE CELL

51. *Nature of the Cell*

The bodies of all living things are composed of units of living matter which are called cells. To put it a little differently, the cell is the morphological and physiological unit of living things. Just as bricks are used for building houses and are the units of the wall, so cells are used for building bodies.

Suppose one were to take a ripe apple and also an imitation apple of wax and break each one open. Then suppose the eye to receive a sudden access of vision which would enable it to see microscopically. The broken wax would appear as a homogeneous mass without any visible details of structure. The apple surface, however, would glisten with thousands of shining bead-like bodies through the transparent walls of each one of which could be seen a granular substance enclosing a globose and denser body. The shining beads are the cells of the apple. They are provided with cell walls enclosing their protoplasm, which is differentiated into a liquid cytoplasm and a denser body called the nucleus. This gives us another definition for the plant cell: it is a unit mass of protoplasm, or it is a mass of cytoplasm enclosing a nucleus and enclosed by a cell wall. With a delicate machine known as a microdissection apparatus, it would be perfectly possible to pierce the cell wall or even to tear it away altogether. Under these conditions the liquid protoplasm or the protoplast, as the fluid mass is called, would exude as a viscid drop of jelly. Its consistency and general behavior would remind us of the white of an egg. Still using the microdissection needles, we could determine that the nucleus could be moved about in the cytoplasm, and that its nucleoplasm was denser and less watery than the cytoplasm. Cytoplasm plus nucleoplasm constitutes protoplasm.

Cells vary remarkably in size. The largest single cell is that of the ostrich egg, which holds about two quarts of liquid. It should be realized, however, that this material is mostly non-living food intended for the nourishment of the chick. At the other extreme come the minute cells of the bacteria. A striking idea of their size may be gained from the statement that 1,000,000,000 bacterial cells could easily be accommodated in one cubic millimeter of water.

52. *The Physical Structure of Cytoplasm*

Under a low power of the microscope, cytoplasm seems to be a homogeneous jelly, but upon the application of higher powers, small granules become visible in it. These are proved by various microchemical tests to belong to different chemical categories, and we will consider them in more detail later. We are now interested in the nature of the cytoplasmic groundwork itself. Under the ultramicroscope ctyoplasm is seen to be made up of myriads of tiny particles seemingly suspended in a homogeneous liquid and all in constant quivering oscillation. The ultramicroscope is an instrument which makes use of the so-called "Tyndall effect" of light. When a ray of light penetrates a darkened room, the path of the beam is made visible by millions of dust particles — the "motes in the sunbeam." We do not actually see the particles of dust; we merely catch the flashes of light reflected from their surfaces. The ultramicroscope is based on this principle of light reflection. A ray of light is admitted into a darkened chamber on the microscope stage where lies the material to be studied. If the system contains tiny particles, each becomes a light center, and their flashes may be seen though they themselves are invisible. Under the ultramicroscope cytoplasm exhibits a brilliant display of flashing points. Our ordinary microscopes can detect bodies as small as 1μ (1 micron or 1/1,000 of a millimeter). The ultramicroscope catches the effect of particles as small as $1\mu\mu$ (a double micron or 1/1,000,000 of a millimeter). The constant quivering of fine particles in liquids is also visible to an ordinary high-power microscope and is due to molecular bombardment. It was first noted by the microscopist Brown, and is called Brownian motion.

53. *Colloids*

The physicist is familiar with a state of matter which gives all the effects which we have just described as characteristic of protoplasm. He knows that if very fine sand is stirred up in water, it remains but a short time in suspension and then sinks to the bottom, leaving the water clear. Such particles may run down to about 1μ in diameter. On the contrary, if fine clay is stirred into water, the liquid remains turbid almost indefinitely and the compound microscope shows the tiny clay particles in rapid Brownian motion. In size they may range from 1μ to about $1\mu\mu$. Matter in this condition is said to be in the *collodial state*, and the system (water and fine clay) is said to consist of two *phases*. The *continuous*, or *outer phase*, is of water; the *disperse*, or *inner phase*, is of clay particles. Such a two-phase system in which the disperse phase is of solid matter is called a *suspensoid colloid*. If the particles fall below $1\mu\mu$ in size, a true solution results.

It is possible through chemical reactions to throw gold into the colloidal condition in water, in which case the two-phase system assumes rich colors running from ruby red to purple, depending on the size of the particles of the gold. The best ruby glass contains colloidal gold. The particles of the disperse phase of a suspensoid colloid bear charges of negative electricity, and many of the curious physical properties of the system seem to depend on this fact. It is found that when salts are added to them the dispersed particles will fall in a gelatinous mass. The reason for such precipitation is to be sought in the activity of the kations of the salts, which discharge the particles of the colloid so that they no longer repel one another. Aluminium trichloride is particularly effective in salting out colloids. It will be noted that its kation bears a triple positive charge.

The enzymatic properties possessed by certain metallic colloids, such for example, as platinum black, may also depend upon the electrical properties of the particles.

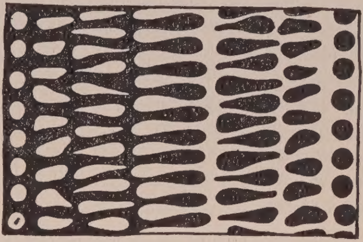

Fig. 78. — Diagram to Illustrate Phase Reversal — the Conversion of an Emulsoid Sol into a Gel. (After Bayliss.)

The most important kind of colloid to the biologist, however, is not the suspensoid, but the *emulsoid*, which differs in the fact that both of its phases are liquids, but liquids which do not mix. Mayonnaise dressing — a vinegar-oil system — is an excellent illustration; so also are milk, cod-liver oil emulsion, and gelatin.

Unlike suspensoid colloids, emulsoids bear relatively weak electrical charges, though they too can be "salted out." They possess strong adsorptive properties, and the liquid particles will pick up on their surfaces whatever suspensoid particles may be present (adsorption). Hence, it is almost impossible to purify an emulsoid. Another property common to emulsoids is a viscous or sticky character.

One of their most conspicuous characteristics, however, is one entitled *phase reversal*. Suppose one dissolves gelatin in water. At first the mixture is a liquid similar to water in consistency. Particles of liquid gelatin are dispersed through the water. In this condition the system is called a *sol*. If one now stands the jar in a cool place, the gelatin soon "sets" to a mass. What has actually happened is this: the gelatin has changed places with the water (Fig. 78). It has become the continuous phase in the form of a foam-like reticulum or mesh-work, while the water is now held in small droplets (disperse phase) in the meshes. In this state the system is called a *gel*. Thus a gel is an emulsoid colloid whose denser component forms the continuous phase. If a piece of gel be dried and subsequently exposed to water, it shows a remarkable power of imbibition or swelling. Water is taken into its intimate substance, and its size increases many fold before it passes again into the true sol state. Dry gel from seaweeds will increase its volume 330 per cent.

All the above discussion of the properties of colloids applies directly to protoplasm, which exists either as "an emulsoid colloid in the sol state" or more commonly, perhaps, as a colloidal gel. Thus, protoplasm shows the ultramicroscopic structure of all colloids; it will not crystallize, nor is it subject to osmosis; it is easily precipitated or coagulated by salts or by heat; it adsorbs foreign particles tenaciously; it imbibes water actively; it often undergoes phase reversal during life, and it assumes the permanent gel state at death (*rigor mortis*).

The above description of cytoplasm has erred on the side of simplicity, and it must be admitted that not all students are agreed even on its fundamental colloidal nature. Furthermore, there is reason to suspect that it possesses a definite structure which our microscopes do not reveal. Wilson says:

> "Up to the present time no single theory of protoplasmic structure has commanded general acceptance, and it is more than doubtful whether any universal formula can be given. We are driven by a hundred reasons to conclude that protoplasm has an organization that is perfectly definite, but it is one that finds visible expression in a protean variety of structures and we are not in a position to regard any of these as universally diagnostic of the living substance."

54. *Membranes and Their Importance*

Protoplasm, like any other liquid, forms surface tension membranes on the boundaries between the phases of its own system or between its own system and any other. Either in water or in air it is covered with a membrane which shuts it off from the surrounding medium. Its nucleus is enclosed in a special membrane, and all its vacuoles (cavities containing liquids) are isolated in like manner. Moreover, if protoplasm is a colloidal gel or sol with a foam-like structure, even the colloidal particles themselves must be enclosed in membranes.

The importance of so many enclosed spaces can scarcely be overestimated. It permits thousands of chemical reactions to go on at the same time in the different parts of the cell, all uninfluenced by one another and yet in contact with the whole cytoplasm through the osmotic interchanges which go on through the enclosing membranes.

55. *The Chemistry of Protoplasm*

Chemically, protoplasm consists of an extremely complex and ever-changing array of proteids with an addition of carbohydrates, fats, ethereal oils, acids, salts, and abundant water; in fact, water is usually so abundant that it has been said that "a plant might be spoken of justly as water held in form by other substances mingled with it" (Barnes). This complex chemical mass is the physical basis — the machine — through which the properties of life are manifested. We may defer to a subsequent chapter the question as to what the term *life* really means.

It should be obvious to the student of chemistry that the synthesis of protoplasm in the chemical laboratory is almost a hopeless dream. The more the chemist knows about it, the more he realizes the tremendous chemical difficulties which would have to be overcome in its successful synthesis. Let it be remembered that protoplasm is the most complicated mixture of chemical compounds known; that its components are fundamentally proteidal; and that no single proteid has as yet been synthesized. Furthermore, let it be realized that if proteids could be synthesized, we would not know which ones are essential to the protoplasmic system or how to throw them into the collodial condition. Finally, the proteids in protoplasm are associated with enzymes, and we have little knowledge concerning enzymes. It is only the ignorant man who talks about "making protoplasm." The problem of its synthesis is a chemical and physical problem baffling in its terrific complexity.

56. *Cytoplasmic Inclusions*

Thus far we have spoken of the cytoplasm as though it were a homogeneous system; this is far from the truth. We suspect, as we have said, that there may be an organization of its fundamental constituents beyond the reach of our microscopes, but however that may be, it is very evident that enclosed in the cytoplasm there are several categories of visible bodies.

A. METAPLASM

The general term *metaplasm* is applied to non-living constituents of the cell. Metaplasm may consist of waste products such as crystals or soluble excretions, or it may be made up of food materials such as oil droplets and starch granules (Fig. 79). Crystals are particularly abundant in plant cells. They are commonly of calcium oxalate or calcium carbonate and are enclosed in small cavities in the cytoplasm which are known as *vacuoles*. Crystals or crystal aggregates sometimes become so large that they almost fill the cell. It must be remembered that the plant, unlike the animal, has no excretory system, and crystals are generally regarded as waste chemical compounds stored in an inactive form.

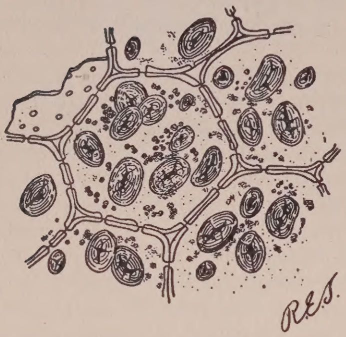

FIG. 79. — Section of a Bean Cotyledon Showing Starch Grains (Metaplasm) in the Cells.

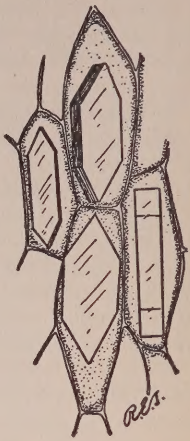

FIG. 80. — Calcium Oxalate in the Form of Tabloid Crystals in the Cells of *Tilia* Phloëm.

In some plants the nucleus plays a prominent part in forming crystals and may actually become enclosed inside a crystalline jacket.

Fig. 80 represents the large tabloid crystals of calcium oxalate which are found abundantly in the inner bark of the linden tree (*Tilia*). Fig. 81 is an aggregate crystal mass (*druse*) from the cell of a petiole of begonia; it is quite probable that the nucleus lies inside it. Fig. 82 represents the cell of an orchid root and shows a set of needle-like crystals of calcium oxalate known as *raphides*. The mass lies

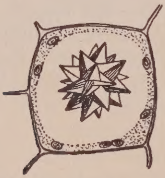

FIG. 81. — Calcium Oxalate in the Form of a Crystal Mass (Druse) from Cell of Begonia Leaf.

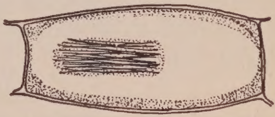

FIG. 82. — Calcium Oxalate in Form of Slender Needles (Raphides) from Cell of an Orchid Root.

enclosed in a mucilaginous sheath. Raphides are extremely characteristics of the arum family; certain members of the *Liliaceæ* are also well provided — notably an onion-like Mediterranean plant, the squill (*Urginea maritima*). Fig. 83 is a curious structure found in some of the epidermal cells of the rubber-plant (*Ficus elastica*), though it also occurs in other plants. The epidermis is two-layered, and it may be seen that one of the inner cells is swollen to accommodate an odd structure which hangs from its roof like a bunch of grapes. The whole body (cell with its inclusion) is called a *cystolith* — literally, "sac-stone." The pendulous mass consists of a stalk and a core of cellulose upon which has been deposited an incrustation of crystalline lime. If one adds a drop of acid to a section of rubber-plant leaf, a lively effervescence of carbon dioxide will be seen.

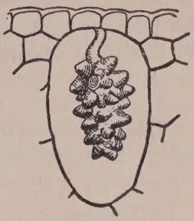

Fig. 83. — A Cystolith from the Rubber-plant. Crystalline masses of lime are deposited around an axis of cellulose suspended inside a cell.

B. VACUOLES

We have spoken already of vacuoles or cavities which occur in almost all plant cells. They are very characteristic structures and should be confused neither with the contractile vacuoles nor the food vacuoles of protozoan animals. The plant cell vacuole is a more or less globose cavity filled with liquid, mostly water, containing acids, salts, and other chemical substances in solution. Sometimes vacuoles are so numerous in the cell that the protoplasm presents a foamy appearance. At other times, and particularly in old cells, a single great vacuole may occupy the middle of the cell, with the cytoplasm reduced to a thin membrane lying against the cell wall. Often, too, under these

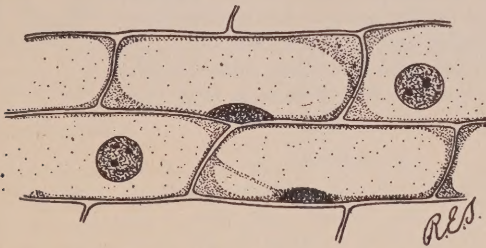

Fig. 84. — Portion of the Inner Epidermis from the Scale of an Onion Bulb. Cell walls, nucleus, cytoplasm, a cytoplasmic strand and sap vacuoles are shown.

conditions, slender strands of cytoplasm will traverse the watery vacuole from one side of the cell to another. The water inside a vacuole is usually under pressure due to the play of osmotic activities; this we shall later consider in more detail. Figs. 84, 85, 86, 87, and 88, all illustrate the vacuolar structure of protoplasm.

C. CHONDRIOSOMES

Chondriosomes constitute a group of bodies found in young cells which seem to be a normal constituent of the cytoplasm. When cells are stained by certain special methods, the chondriosomes appear variously as minute dots, rods, or threads (Fig. 85). It is claimed that they have been seen in active motion in living cytoplasm, and furthermore that they change their shapes as they move, now tapering to threads, now shortening to rods or club-like bodies, now constricting to the dumb-bell form. Biologists are not at all agreed as to their nature or function.

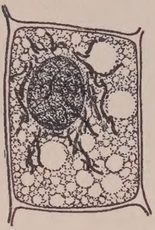

FIG. 85. — Chondriosomes in a Young Plant Cell. The highly vacuolar nature of the cytoplasm is also evident.

Professor Wallin * has suggested that they may even be bacteria living in symbiosis with the cytoplasm. Building upon this idea, he advances the hypothesis that the nucleated cell itself has arisen in evolution from the symbiotic association of bacteria which have become merged into a single protoplasmic mass, and that its subsequent evolutionary changes may have been caused by the invasion of new strains of bacteria from time to time.

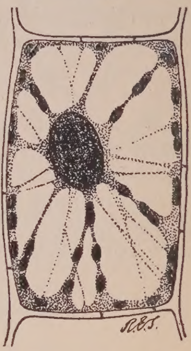

FIG. 86. — A Single Cell of a Hair from a Squash Stem Showing Nucleus Suspended by Cytoplasmic Strands in a Central Sap Vacuole. The chloroplasts are represented in silhouette. In the living cells of this plant the cytoplasm shows active streaming motion.

D. PLASTIDS

The most conspicuous structures in many plant cells are the *plastids*. The term is applied to differentiated portions of the protoplast which are concerned with special physiological activities. It is not easy to give a strictly morphological definition of them, since they vary much in form. The most common plastid is the *chloroplast* — the green body which gives the green color to vegetation. In its typical form it is an ellipsoid or globose body, and the average cell contains several scores of them (Figs. 86, 87). If instead of the piece of apple which we examined with microscopic vision, we had chosen a fragment of a green leaf, we should have seen through the transparent cell wall many small, brilliant green chloroplasts in addition to the granular cytoplasm and the nucleus. The chloroplasts of some plants possess odd shapes. In certain algæ they have the form of spiral ribbons or of elaborately folded star-shaped bodies (Figs. 88, 89, 90).

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* I. E. Wallin, *Symbionticism and the Origin of Species* (Baltimore, 1927).

If we immerse a green cell in alcohol, we find that the green coloring matter can be dissolved out of the chloroplasts, leaving them white. Thus we come to realize that the plastid itself is not green but is a colorless proteidal body which holds in itself the green pigment — *chlorophyll*. In certain parts of plants which are hidden from the light, only white plastids are to be found; when exposed to the light, chlorophyll appears in them and they become green. Such white plastids are called *leucoplasts*. An instance of the transformation of leucoplasts into chloroplasts is familiar to all farm boys. Potatoes in the hill turn green when exposed to the light; their leucoplasts have developed into chloroplasts.

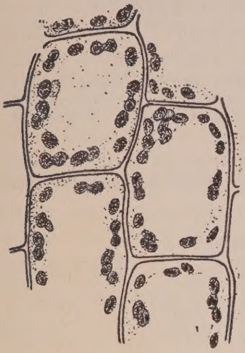

FIG. 87. — Several Cells from the Leaf of a Water Plant (*Elodea*). Tiny starch grains associated with the chloroplasts are represented in black. Active rotation of the cytoplasm makes this plant a classic for studies in the physiology of protoplasm.

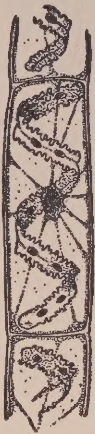

FIG. 88. — Cells of a Filamentous Alga, *Spirogyra*, Which Takes Its Name from Its Spiral and Ribbon-Shaped Chloroplasts. These may vary in number from one to many in the cell.

Plastids may also carry pigments other than chlorophyll. In the brown and red algæ the pigment is brown or red and the plastids are called respectively *phæoplasts* and *rhodoplasts*. Bright petals of flowers may also carry colored plastids which take the collective name of *chromoplasts*, though the colors of flowers are more often due to the fact that the cell sap in their vacuoles bears a colored compound (anthocyanin) in solution.

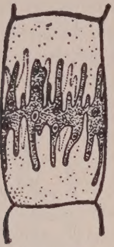

FIG. 89. — A Cell of the Filamentous Alga *Oedogonium*. The chloroplast is an equatorial ring with elaborately fringed edges.

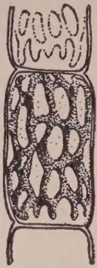

FIG. 90. — A Cell of the Filamentous Alga *Cladophora*. The chloroplast is a hollow cylindrical net.

E. THE CENTROSOME

The centrosome (Fig. 91) is a small granule associated with the nucleus in all animal cells and in the cells of the lower plants. It is not found in the flowering plants. When present it plays a prominent part in the process of nuclear division.

57. *The Nucleus*

The nucleus is the most important protoplasmic mass in the cell. It is extremely complex in structure, and its activities present numerous baffling problems. Physically, it is commonly a transparent globose or ellipsoid body, larger in young cells than in old ones. It is surrounded by a tough, nuclear membrane and contains a clear, watery nuclear-sap or *karyolymph*. Running as a network through the nucleus there seems to be a mass of fibrous material called *linin* or *achromatin*, while upon and through this network are massed and scattered numerous granules of *chromatin*. In addition, one to several gleaming *nucleoli* are usually present in the nucleus (Fig. 96, A).

Before going further a few words are necessary to explain the methods used in the investigation of nuclear and other protoplasmic details. Under a high power of the microscope the nucleus appears as a granular mass in which the nucleoli gleam brightly; little more can be seen. If, however, the cell be immersed in certain dyes and later examined, it will be found that definite structures in the cytoplasm and in the nucleus have stained with great brilliancy, while others are almost unaffected. Suppose we use the red aniline stain safranin; the chromatin takes up the stain with avidity, but the achromatin is almost unaffected. In fact, it is this very characteristic of taking up stains that has given the chromatin its name from the Greek (*chroma* = "color"), whereas, the term *achromatin* signifies "without color."

A. THE CHEMISTRY OF CHROMATIN

Chromatin is the most significant substance in the nucleus. It is essentially the germ-plasm and is the substance handed down from parent to offspring in reproduction. An oak-tree differs from a toad-stool because the chromatin in the cells of the oak-tree is different from that in the cells of the toadstool. How an oak-tree or an elephant can be locked up inside a bit of matter smaller than the head of a pin we have no idea, though theories are not wanting whose specious nature is all too easily overlooked. The head of the male element, or sperm of animals, is composed of almost pure chromatin. It is possible to collect sperm in quantity from male fish at the breeding season. The vibratile tails of the sperm can be centrifuged off and then the chromatin collects at the bottom of the jar in the form of a whitish gel. Under chemical analysis it breaks down into two final major constituents called respectively *nucleic acid* and *protamine*. Nucleic acids derived from all fishes are either identical or very similar in composition. As an illustration of its complexity, we may say that there have been recognized in nucleic acid the following compounds: two purine bases, guanine and adenine; two pyrimidine bases, thymine and cytosine; a hexose; and phosphoric acid. One German worker gives the chemical formula as $C_{40}H_{56}N_{14}O_{16}, 2P_2O_5$.

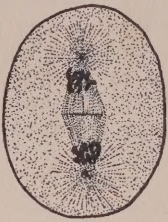

FIG. 91. — Single Cell from a Fern in Process of Nuclear Division. The polar dots whence proceed the radiations are the centrosomes. These bodies do not occur in seed plants.

The protamines are the simplest known proteids, and those from different fish are all different. Thus from the codfish (*Gadus*) comes a protamine which has been called gadin; from the herring (*Clupeus*) one called clupein; from the salmon (*Salmo*) one known as salmin. We may think of chromatin, then, as in large measure made up of protamine nucleate; it is a nucleo-proteidal salt.

To say, however, that species differences among organisms rest upon such a simple chemical basis is undoubtedly too naïve an explanation.

In the nucleus, as in the cytoplasm, there are many enzymes — those mysterious, probably colloidal bodies which act by catalysis to bring about chemical reactions in substances with which they come into contact. Biochemistry finds itself confronted with such catalyzed reactions at every turn, for one of the striking facts about organisms is the prevalence of enzymatic activities in their bodies. It is likely that the nuclear sap contains hundreds of specific enzymes. For that matter, we may finally discover that the phenomena of physical heredity rest upon the enzymatic properties of chromatin.

The nucleus is essential to the life of the cell. Certain low forms of animal and plant life are unicellular. If with delicate instruments we destroy the cell nucleus, the cell will die; if the cell is cut into two parts, the enucleated fragment dies. If, however, the nucleus itself is cut in half by the section, then both fragments of the cell will continue to live.

58. *The Cell Wall*

Thus far we have spoken only of the structure of the protoplast. In animal cells this is enclosed in a delicate membrane of proteidal material, but the plant cell is provided with a definite wall which in its primary condition consists largely of a carbohydrate compound called *cellulose* $(C_6H_{10}O_5)_n$. Cellulose is manufactured and secreted by the protoplasm. In its unmodified condition it is hyaline and transparent, but it often becomes infiltrated with other compounds and then gives other chemical reactions. Cotton, which consists of the dead thin walls of the hairs which cover the cotton seed, is almost pure cellulose. Paper, too, is another fairly pure example of the compound.

As we shall learn shortly, cells increase in number by division of the protoplast. The septum which first arises between the two resultant cells is common to both and is a product of their joint activity. Very soon, however, each new cell begins to secrete layers of cellulose, and thus the original septum comes to form a common binding membrane between them. This membrane takes the name of the *middle lamella*. It differs chemically from cellulose in being a pectic or gum-like substance. It can be dissolved by certain reagents and thus the cells of a tissue may be isolated from one another (*maceration*).

Cell walls usually undergo secondary chemical modifications which are due either to the infiltration of new compounds into the old cellulose wall or to the deposition of new compounds in layers on the inside of the primary wall. Thus arise woody or *lignified walls*, corky or *suberized walls*, *cutinized walls*, *silicified walls*, and *calcified walls*.

Sometimes water enters abundantly into the wall substance, which may then become *gelatinous* or *mucilaginous*.

So long as the cells in the plant body remain alive, their protoplasts keep up organic connection with one another. In order that the cell walls may not cut off these connections, certain tiny areas remain unthickened and serve as pores through which threads of cytoplasm pass from cell to cell. These pores are called *simple pits*. In cases where the cell walls become very much thickened, as they do in peachstones, shells of nuts, etc., the simple pits appear as numerous fine tubular canals running from one cell to another. It is evident that in the formation of pits the protoplasm fails to deposit the layers of wall material in certain small, definite regions which consequently remain like tiny port-holes in the wall.

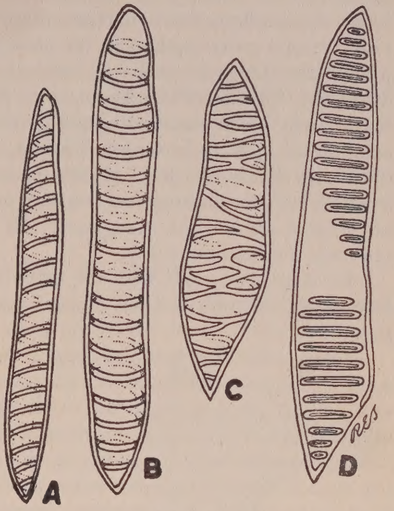

Fig. 92. — Four Cells Taken from Wood to Show Various Types of Cell Wall Modifications. A, B, C, D, represent respectively the spiral, annular, reticulate, and scalariform type of wall thickening.

The middle lamella is not perforated by the simple pit, but remains instead as a delicate *pit membrane*. High magnification shows that this membrane itself is traversed by minute pores through which run fine cytoplasmic threads. Fig. 99 is a drawing of dead cells of elder pith whose thin cellulose walls bear simple pits.

The simple pit is one of the simplest forms of cell wall modification. Quite commonly much more elaborate sculpturings are introduced. One very prevalent type, particularly on woody cells, is the *spiral thickening*. Here the protoplasm lays down material in the form of a spiral band along the wall (Fig. 92, A). Slight modifications convert the spiral thickenings into the *annular*, the *reticulate*, or the *scalariform*. In the first, the inside of the wall bears successive projecting rings (annuli) which resemble barrel-hoops (Fig. 92, B); in the second, the wall is covered with a netted system of strands (Fig. 92, C); in the third, a ladder-like effect is produced by the regular arrangement of straight thickened bars which lie one above another like the successive rungs of a ladder (Fig. 92, D). There is one more type, most common of all in woody tissues and known as the *bordered pit*, whose consideration we will defer till we come to the study of wood.

It has long been known that the walls of plant cells are neither physically nor chemically homogeneous. Under high magnification their cross-sections show evidence of lamination and their surfaces exhibit delicate cross-markings. We have already noted that the simple pits of the elder-pith cell wall have their long axes oriented in one direction. This forcibly suggests that the pits are only places where the threads of wall substance, which are responsible for the striations, are pushed apart. In decay, likewise, wood fibers develop myriads of oblique slits in the wall. All this goes to show that the walls possess some sort of fibrous structure and are not mere amorphous envelopes of cellulose around the cytoplasm. All these details are revealed by ordinary microscopic study.

Recently, in accord with the drive along all scientific fronts into finer fields, the cell wall has yielded evidence of its ultramicroscopic structure.

About 1860 the botanist Nägeli suggested that organic bodies such as starch grains and cellulose walls are composed of minute units which may be regarded as of the nature of ultramicroscopic crystals, and which he called *micellæ*. Nägeli furthermore suggested that the micellæ are surrounded by films of water and that the swelling of such substances is due to the pushing apart of the micellæ when more water enters the interstices between them.

Recent researches * with X-rays and with polarized light have shown that the micellæ really do exist, though the substance between them is a "hydrophilic phospholipoid" rather than pure water. It seems to be continuous with a thin film which surrounds the cytoplasm. The young cell wall, then, is a physiologically active membrane, and one researcher has gone so far as to assert that the wall, like the protoplasm, is alive. The micellæ of cellulose are themselves said to be about 60$\mu\mu$ long by .5$\mu\mu$ in thickness, and seem to be ellipsoidal in shape. They are built up of glucose rings arranged end to end, and about sixty of these macro-molecular chains are combined into one micella. Here is the ultimate basis for the remarkable tensile strength which plant fibers possess.

Even as the molecules are organized into chains within the micellæ, so the micellæ, in their turn, are generally arranged in fibrils within the cell wall. It is the effect of the strings of micellæ that our microscopes reveal as striations, slits, etc. In the bast fibers of flax, these fibrils run in a steep spiral which changes its direction in successive layers of the wall; in cotton the spiral appears to reverse its direction at various nodal points in the same layer. In sieve cells, however, where no great tensile stresses develop, the micellæ seem to be scattered about without any definite fibrillar arrangement.

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* D. B. Anderson, "Some Recent Work on the Structure of the Plant Cell Wall," *Ohio Journ. Sci.*, XXVIII, 299–312, 1928.

Kurt H. Meyer, "The Molecular Structure of the Cell Wall," *New Phytol.*, XXX, 1–10, 1931.

The matter is obviously one that carries us to the border-line of optical research. It shows the remarkable technical advance which physics is making, and it quite changes our concept of the nature of the cell wall. The micellæ may even have to be regarded as living units. There is considerable evidence that living things far smaller than the cell exist, and that the cell itself is but one in an ascending series of hierarchical "lives."

59. *The History of Cytology*

In 1665, Robert Hooke, an amateur who had been playing with the microscope, published a book which he called *Micrographia, or Some Physiological Descriptions of Minute Bodies Made by Magnifying Glasses with Observations and Inquiries Thereon.* In ths book there appeared for the first time rather crude drawings of cells (Fig. 93). Hooke had been "slicing up indiscriminately animal and plant tissues" and while examining charcoal, cork, and other substances, he saw that they were "all perforated and porous, much like a honeycomb." It is said that he gave the term *cell* to the little cavities because they reminded him of the cells in monasteries (from Latin *cella*, akin to *celare*, "to hide"; a very small and close apartment in a monastery or convent).

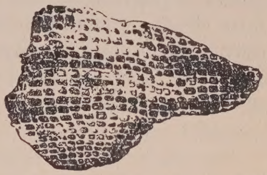


FIG. 93. — Cells of Bottle Cork from Hooke's *Micrographia* (1665). This is the first figure of cells ever published.

The first idea of cells was the wholly mistaken one that the wall system or *interstitia*, as Hooke called their substance, was the living part and that the cavities were only for the circulation of juices. This makes it clear why the early histologists were so fond of comparing plant tissue to fine lace — in fact the word *tissue* originally meant a woven cloth.

As the years went by, this concept slowly changed, and the individual cell wall came to be looked upon as the cell and not as a mere living substance between cells. This, too, was a false view, for thus far everything inside the cell wall was called "nutrient sap" or "vital juice" and considered of little importance. It was not till 1831 that Robert Brown, who it will be remembered was also the discoverer of "Brownian motion," saw and named the nucleus. So it happened that the nucleus was discovered before the cytoplasm.

The zoölogists really appreciated the true nature of the cell before the botanists. Dujardin, in working on the protozoa, applied the name *sarcode* to the substance of their bodies; Purkinje, a human physiologist, in 1840, gave the name *protoplasm* to the substance composing human cells; and in 1844 the botanist Von Mohl took the plunge and boldly announced that the slimy lining of the vegetable cell was a living substance and was the primary and most important constituent of the cell. He gave it the name *protoplasm*, adopting Purkinje's term. Later, when it was realized that certain cells might exist without walls, the whole concept of the cell changed to the modern accepted view: the cell is a unit mass of protoplasm with a nucleus, and the cell wall is non-essential.

The above discussion of the early history of cytology illustrates very well the way in which a scientific concept progresses toward truth. After imperfect observation and faulty interpretation, a theory is propounded; other workers try to check it up and discover facts which are not in accord; thus the theory is modified over and over again until at last all are agreed that their own experience tallies. Then the theory takes its permanent place in the body of accepted scientific generalizations.

CHAPTER XI

THE ACTIVITIES OF THE CELL — PHYSIOLOGY

With some knowledge of the cell machine, we are now in a position to consider its activities or its physiology. Here again, we encounter baffling problems the solution of which must rest upon the united labors of future generations of biologists. The following treatment must be very general.

Speaking broadly, all the multifarious physical activities of organisms are summations of the activities of the cells which make up their bodies. If a muscle contracts, it is the summation of the contraction of many muscle cells that is manifested; if a green leaf swings toward the light, it is the coöperative activity of the constituent cells which produces the movement. Hence, the cell is the place where we must study the functions in their unit expressions.

60. *Osmosis, Turgor, and Diffusion*

One of the most fundamental energy manifestations of the plant cell is expressed by the term *turgor*. All are aware of the difference in appearance between a fresh and a wilted plant. The tissues of the former are said to be turgid — of the latter, *flaccid*. The difference depends entirely upon the difference in water content of the cells.

Some pages back it was pointed out that the ordinary plant cell contains vacuoles filled with watery cell sap; in old cells the vacuole is usually single and large, so that it occupies the whole middle of the cell and forces the protoplasm outward till it assumes the form of a thin film resting against the cell wall. *This thin protoplasmic film or layer, sometimes called the primordial utricle, behaves like an osmotic or semipermeable membrane.*

A. PERMEABLE AND SEMIPERMEABLE MEMBRANES

In relation to the passage of water and salts, two sorts of membranes may be distinguished, permeable and semipermeable. The *permeable* membrane is one which offers little resistance to the passage of solutes or of water. Suppose, for example, a solution of common salt be place in a tough paper bag and suspended in a jar of water. A process of diffusion begins at once. The salt passes with little hindrance into the water outside the bag, while water from outside passes into the bag, till finally an equilibrium is established.

Such movements of diffusion are explained by the kinetic theory of matter, which teaches that the molecules or ions of both salt and water are in active vibration and consequently tend to spread in all directions. The cell wall of plants cells, like the paper bag, is a permeable membrane and offers little or no resistance to the passage of water and salts.

The physicist is familiar with another kind of membrane which he calls *semipermeable.* If we take a piece of bladder membrane or a piece of gold-beater's skin derived from the intestine of the ox, make a small sac out of it, fill it with salt solution, and suspend it in water, we will soon observe a curious phenomenon. The sac begins to swell, or becomes turgid, and finally the pressure inside may rise so high that it will burst open. If, instead of closing the mouth of the sac, we had tied it firmly to a long glass tube with a narrow bore, we should have seen the water rise slowly in the tube, as the turgor pressure developed inside the sac, till it might have attained a height of a meter or more.

The physical explanation of this osmotic activity is not an easy one. The passage of water through the membrane into the salt solution may be a mere diffusion phenomenon, but why it becomes trapped there and increases the turgor pressure we do not know. We can only say that when two liquids of different densities (viz., containing different quantities of solute) are separated by a semipermeable membrane, then water passes from the less dense to the more dense solution.

Suppose we reverse the experiment outlined above. Let us fill the osmotic apparatus with fresh water so that the water rises a few feet in the attached tube and then plunge the sac in salt solution. Right away the water level begins to fall in the tube and finally the sac itself may become limp and flaccid. The explanation is obvious; the pure water inside the apparatus has moved out through the membrane to a point of greater concentration of salt. Such an outward movement is called *exosmosis* as opposed to the movement inward, which is termed *endosmosis.*

All these physical facts are applicable to the passage of water into and out of cells. The cell wall, as has been said, is a permeable membrane; the layer of protoplasm or primordial utricle which lies just inside the cell wall is, on the contrary, a semipermeable membrane. It separates the sap of the vacuole from water outside the cell. The cell sap is never pure water but contains sugar and various salts in solution. It is obvious, then, that if a cell is submerged in water, there is bound to be a passage of water through the protoplasmic membrane into the vacuole (endosmosis). Then the turgor pressure rises and the cell becomes inflated like a toy balloon into which air has been forced. If we now think of the single cell as a unit among thousands of other cells, all together forming a plant tissue, it is easy to see that the reactions of their elastic walls against one another will give a firmness and rigidity to the whole tissue, whereas a loss of water by evaporation reduces the turgor pressure, leaving the tissue wilted.

B. PLASMOLYSIS

The above discussion is concerned with endosmosis, but the reverse process or exosmos also goes on and is easily brought about artificially. If a thin section of beet-root be placed under the microscope and irrigated with salt solution, one can witness a phenomenon known as *plasmolysis*. As the water begins to leave the vacuole and the turgor pressure falls, the elastic protoplasmic membrane begins to contract and to pull away from the cell wall. If the action continues long enough, it may pull away so completely that it assumes the form of a hollow sphere — like a shrunken toy balloon — in the middle of the cell. Cells in this condition are said to be *plasmolyzed*. If the tissue be placed in fresh water again, endosmosis once more starts up, since now the stronger solution is that of the concentrated sap of the vacuole. Within a few minutes the resulting turgor pressure pushes the membrane out against the cell wall again. Fig. 94 illustrates this series of events.

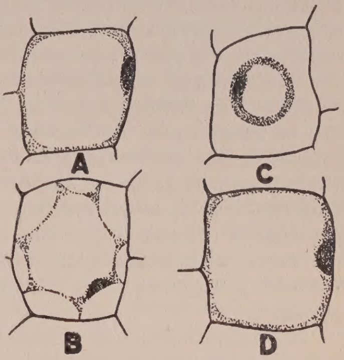


FIG. 94. — Plasmolysis in the Beet Cell. A, cell in normal condition; B, after short treatment with salt water; C, after prolonged treatment with salt water; D, after restoration to fresh water.

We sometimes say that strong fertilizers " burn roots "; it will be clear to the student that intense exosmosis is set up, so that the cells are plasmolyzed and finally die.

C. THE DIFFUSION OF SALTS THROUGH SEMIPERMEABLE MEMBRANES

Thus far we have spoken only of the passage of water through semipermeable protoplasmic membranes. Yet there is no membrane known which is truly semipermeable in the sense that it permits the passage of water only. Suppose our endosmosis apparatus has been standing for some time immersed in water which was fresh at the beginning of the experiment. A test with silver nitrate will show that salt has diffused through the sac and into the water outside. The passage of salt will continue until equilibrium is established. Then there will be the same amount of salt both inside and outside the sac. Of course the diffusion of salt can be easily brought about by suspending a sac of fresh water in a vessel of salt water.

We are in a position to understand now how a single cell living in water can obtain the salts out of which it must manufacture its foods. Suppose we take a one-celled plant whose content of any salt — let us say potassium nitrate — is negligible, and place it in pond water. Potassium nitrate exists in such water in minute quantities, and this salt begins at once to diffuse through the membrane. In a little while equilibrium will tend to be established. But suppose that, as fast as the salt enters, it is precipitated as an insoluble compound. This will effectively remove it from solution, and thus a constant ingress can be maintained. This method of keeping up a constant inward passage of salt has been demonstrated for some plants. If a floating water plant, the duckweed (*Lemna minor*), is placed in an extremely dilute solution of methylene blue, it takes up so much of the blue dye that it becomes bright blue. It has been discovered that the dye reacts with tannin in the cells to form an insoluble compound which is precipitated from the solution; thus, equilibrium is never attained.

In multicellular plants equilibrium is prevented in the absorbing cells by relaying the absorbed salts from cell to cell to their final destination, where they are utilized in food manufacture and removed from solution. It is evident that, in a system of cells whose terminal members never attain equilibrium, a constant ingress and movement of salts from cell to cell is bound to go on.

D. THE LIVING PROTOPLASMIC MEMBRANE

Thus far we have discussed the osmotic properties of cells as if we were dealing with dead osmotic membranes. This, however, is far from exact. The protoplasmic membrane is a living, colloidal, organized membrane and its permeability to salts is widely variable. One plant may absorb quantities of silica from the same soil from which another takes lime or magnesia. Protoplasm, then, has the power of *selective absorption*, and this varies to a large extent, not only with different plants but with the same plant at different times. It seems also to depend partly upon the types of electrolytes present in the water. Certain anions or kations increase or decrease the permeability of the membrane to certain other salts. While we believe that the phenomena of water absorption and salt absorption are essentially physical phenomena, we must confess that the full explanation of these activities belongs to the biology of the future. We realize that the solutions both inside and outside the membranes are always changing and that the membrane itself is a living complex of organized colloidal matter constantly undergoing modifications due to its own chemical activities and to the influence of outer conditions.

61. *Metabolism*

In order to live, it is necessary that protoplasm should have food-salts and water. We have seen how these enter the cell; it now becomes our problem to see how they are converted into foods to be utilized in the building-up of new protoplasm, which is subsequently broken down as energy is released.

The whole process to which reference has just been made — the series of chemical changes which foods pass through after being absorbed by the protoplasm — is called *metabolism*. Or metabolism may be defined as "the chemical changes proceeding continually in living cells by which energy is provided for the vital processes and new material is assimilated to repair the waste." There are evidently two parts to the process: first, a series of events by which simple substances are built up into more complicated ones, and second, a process of breaking down, through which complex substances are resolved into simpler ones. The first is called *anabolism* (*ana* = "forward" or "up" + *ballein* = "to throw"); the second constitutes *katabolism* (*kata* ="down"). The metabolic process may be divided into the following successive steps: ingestion, digestion, absorption, egestion, and excretion. The first step — true *ingestion* — scarcely ever occurs in plants. It is a term applied to the taking in of solid matter and can only go on when there is no cell wall, as in an amœba, or when a definite cell gullet is provided, as in *Paramœcium*. It is evident that ingestion is a characteristically animal method of taking food.

Digestion follows ingestion: it is simply the process of converting the food into a soluble state. Digestion may sometimes go on outside the cells as it does in the pitcher-plant (*Sarracenia*), which digests the dead insects drowned in the water of its pitchers. More often, however, it is an intracellular process. Many plant cells store up quantities of solid food against a day of need. This must be digested before it can be utilized. Digestion in plant cells usually goes on in vacuoles and is dependent upon the activity of enzymes.

Solid foods having been digested, they are ready for *absorption* into the cytoplasm in accordance with the principles of diffusion already familiar to the student. Their atoms are then recombined into new compounds and the cell grows. *Growth*, if by the term we mean mere increase in size, does not necessarily mean increase in the amount of protoplasm. A flaccid cell grows when placed in water. A striking example of this kind of growth is that of the mushroom, which forms in miniature beneath the soil even in dry weather. Upon the advent of rain it swells enormously and grows up overnight as if by magic. The *primary* synthesis of such solid foods as go to the increase of the amount of protoplasm will be considered when we come to study the leaf. It is sufficient at this point to say that the chemical compounds which are absorbed by the plant cell are usually very simple inorganic salts or gases. They possess but little internal energy and are very stable. The substances which constitute protoplasm, on the other hand, are made up of complex organic compounds with giant molecules and great quantities of latent energy. The molecules are very labile and break up easily under the activity of enzymes, thereby setting their energy free to be utilized in the work of the cell.

The katabolic processes connected with the decomposition of organic molecules are intimately associated with *respiration*. Respiration is an activity that proceeds constantly in living matter and is, in fact, the best test that we have to show whether an organism is dead or alive. Oxygen is taken into the protoplasm and carbon dioxide is eliminated, while at the same time energy is released in one form or another. Katabolism — this process of tearing down protoplasmic compounds in order to gain energy — produces waste substances in the cell. These are often deleterious poisons which must not be permitted to accumulate. In animals they form the excretions, but in plants, since there is no active excretory system, they are often stored in vacuoles in the form of inactive crystals.

A careful distinction must be maintained between secretions and excretions. *Secretions* are substances given off from protoplasm which have a rôle to perform in subsequent metabolic activities. *Excretions* are katabolic wastes which are of no value to the organism. Saliva, gastric juice, and bile are secretions from our own cells, while perspiration and urea are excretions. *Excrement*, on the contrary, is the undigested residue of ingested foods; it has never been an actual part of the protoplasm at all. Naturally only the very lowest of animal-like plants can egest excrement, since they alone ingest solid food.

62. *Irritability*

We are now in a position to think of the protoplasmic system as a delicate and labile mechanism easily modified by both the inner forces of its own system and the outer forces of its environment. The property which protoplasm possesses of responding to external influences is called *irritability*. The manifestation is initiated by a *stimulus*, and the evident change itself is called a *response*. A response may show itself as a movement, a rise in temperature, a change in the electrical state, or even a flash of light. Protoplasm reacts to almost every physical stimulus. When the response is expressed as a movement, it is called a *tropism* (Greek *tropein* = "to turn"). If the tropism is such as to orient the protoplast so that it receives the stimulus more intensely, it is called a positive tropism or *protropism;* if, on the contrary, the protoplast reacts away from the stimulus, the reaction is called a negative tropism or *apotropism.*

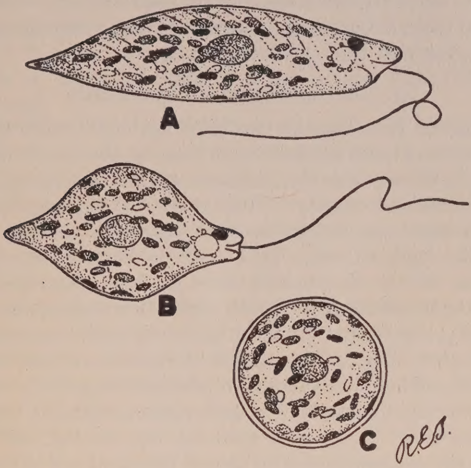


FIG. 95. — A Unicellular, Green, Motile Plant-Animal (*Euglena viridis*): A, in the active swimming state; B, exhibiting a "euglenoid contraction"; C, in the encysted state in which the organism usually passes the winter. Details of cytology shown are the anterior flagellum, the cell-gullet, eye-spot (stigma), contractile vacuole, nucleus, chloroplasts, and striated cuticle.

In most cases tropismic responses place the protoplast in conditions more favorable to its optimum biological activities. An illustration will make this clear: certain green algæ are unicellular and are provided with vibratile, swimming cilia (Fig. 95). If a jar of water containing them be placed in darkness, the small organisms distribute themselves equally through the jar. Now remove the jar to a lighted window and from all sides the tiny green cells swarm toward the light. They are manifesting *positive phototropism.* Their tropism can be reversed, however, for if the strong glare of an arc-light be brought to play on them, they will turn precipitately and beat a retreat; they have become *negatively phototropic.* Such movements look as though they were directed by purpose and will, but it will be shown subsequently that this assumption is not necessary to an explanation. A plant grown in a window becomes one-sided because the combined activities of the strongly phototropic cells swing the whole system into the best light relation.

These illustrations based on phototropism will make clear the terms *chemotropism* (response to chemical substances), *geotropism* (response to gravity), *stereotropism* (response to solid bodies), *electrotropism* (response to electric currents), and *rheotropism* (response to flowing currents of water).

63. *Contractility and Conductility*

If protoplasm is to respond to stimuli by means of movements, it must be contractile and conductile; it must be able to shrink its mass or parts of its mass to smaller compass, and one part must be able to pass on the stimulus to another. These properties of protoplasm are not so evident in plants as in animals, since their manifestation is usually limited by the rigid cell wall. Yet among the lower forms of plant life and even in certain of the high ones, such as the sensitive-plant (*Mimosa*), the manifestation of both contractile and conductile properties is hardly inferior to that of the hydrozoan polyp among animals. The tiny *Euglena* (Fig. 95) is capable of vigorous contractions. It is in the muscle cells of animals that we observe the extreme specialization of the contractile property of protoplasm, while the nerve protoplasm is specialized in an analogous manner for the conduction of stimuli. In the discussion of structure of the plant cell it was pointed out that no protoplast is isolated from its fellows: all are connected by fine cytoplasmic threads, and it is along these living wires that stimuli sweep from cell to cell.

64. *Reproduction*

The millions of cells which make up the body of one of the higher plants have all come from one cell which started that particular ontogeny. One more activity, then, must be added to the functions of protoplasm: it is reproductive. The simplest and commonest method of reproduction is by *division.* Nucleus and cytoplasm become equally partitioned; a new cell wall is laid down through the middle of the cell, and as a result two cells arise from one. Here again we are to strike a tangle of perplexing problems the solution of which will strain the best resources of future optics and technique, for now we are to enter the domain of the nucleus, whence the governance of the cell proceeds and where the secrets of heredity lie hidden.

It is only rarely that the nucleus divides by a simple process of constricting into two parts. This method of division seems to be off the direct highway of normal events; it sometimes characterizes old and weakened cells. It is called *direct nuclear division* or *amitosis*.

A. MITOSIS, KARYOKINESIS, OR INDIRECT NUCLEAR DIVISION

Most nuclei divide by an elaborate process called variously *mitosis*, *Karyokinesis*, or *indirect division*. The first term comes from the Greek *mitos* = "a thread," since in the process the chromatin takes the form of threads; the second term is derived from the Greek *karyon* = "a nut" (a term used as a combining form to mean "nucleus") and *kinesis* = "energy," since it is essentially a manifestation of nuclear energy.

We are already familiar with the nucleus in its so-called resting condition — a misnomer, since only dead nuclei are at rest. In this state its chromatin is scattered about as a network (Fig. 96, A). As the nucleus prepares to divide, the chromatin network resolves itself into a long coiled thread (*spireme*) which soon splits transversely into a definite number of shorter segments, or the network resolves itself directly into a number of reticulate units which pass through stages of condensation till they finally become the same short segments as arose in the first case from the spireme (Fig. 96, B, C, D, E). These segments are called *chromosomes*. Each chromosome now begins to show a longitudinal cleft, marking a line through which the chromosome is subsequently to split into two equivalent longitudinal halves. The chromosomes move to the equator of the cell, where each becomes a curved body shaped something like a horseshoe. They lie in a single plane with loops directed inward and shanks pointing outward.

Meanwhile, other changes have been proceeding in the nuclear region. If a centrosome is present, as it is in the lower plants and in all animals, it divides and its halves begin to diverge from one another. Fig. 96 represents the process as it goes on in a higher plant where centrosomes and asters do not appear. (Cf. Fig. 91.) Around each centrosome appears a delicate fibrillar radiation (*aster*), and in addition a barrel-shaped mass of similar fibrils develops between the two centrosomes and constitutes the *achromatic spindle*. By this time the nuclear membrane has dissolved, and the fibrils now enter the nuclear field, where part of them, at least, become attached to the chromosomes. At this stage the whole karyokinetic figure consists of two centrosomes with their asters, the connecting spindle, and the chromosomes, which lie in a single plane at the equator (Fig. 96, F). Now the longitudinal cleft in the chromosomes becomes more evident

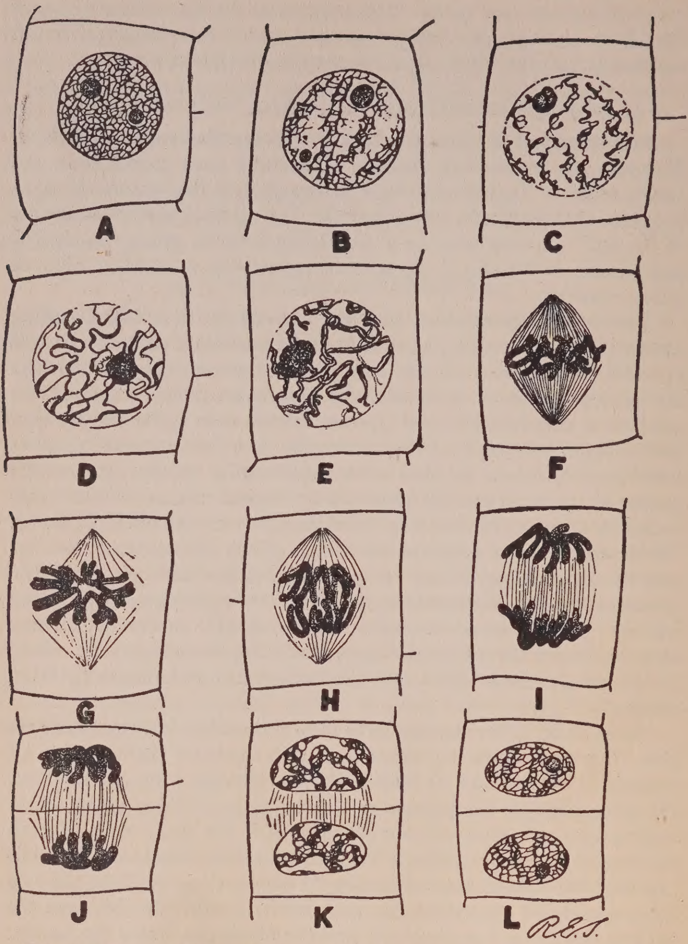


FIG. 96.—Diagram of Successive Stages in Mitosis. The diagram is based on conditions in the flowering plants where neither centrosomes nor asters appear. Explanation in the text.

(Fig. 96, G); each separates into two halves which seem to be drawn by certain of the spindle fibers toward the poles (Fig. 96, H, I, J). It is certain that not all of the fibers are attached to the chromosomes, for they are still visible at the equator after the chromosomes are gone. Reaching the poles, the chromosomes become thicker and stouter. Vacuoles appear in them and slowly increase in size. The vacuoles finally rupture their boundaries and convert the chromosomes into irregular netted bodies which soon became so massed together that their individual limits cannot be seen. Around the whole mass a nuclear membrane appears, and nuclear division is accomplished (Fig. 96, K, L).

While the nuclei are being reorganized, one sees tiny thickenings appearing on the threads of the spindle which still linger at the equator of the cell. These finally coalesce, and the result is a delicate cell wall which cuts the cytoplasm into two parts. Thus, two new cells have come into being.

The process of mitosis just described is divided into certain stages or phases for convenience of study. These are known as the *prophase*, *metaphase*, *anaphase*, and *telophase*. The *prophase* includes all the changes which run from the beginning of the process to the formation of the equatorial plate; the *metaphase* is the equatorial plate stage itself; the *anaphase* includes all events from the separation of the chromosomes till they reach the poles; while the *telophase* consists of the series of regressive changes and vacuolization which brings the resting nucleus into being once more.

The whole mitotic act has been timed in a few cases. In 1917, it was reported that the time consumed in the process, as it goes on in dividing chick cells, is as follows: prophase, 5–50 minutes; metaphase 1–15 minutes; anaphase, 1–5 minutes; telophase up to completion of cell division, 2–13 minutes; reconstruction of daughter nuclei, 30–120 minutes. This gives a total of 70–180 minutes for a mitotic division.

B. MITOSIS IN THE HIGHER PLANTS

As we have said, the details of mitosis, as given in the preceding treatment, do not apply strictly to the higher plants. The main difference is associated with the lack of a centrosome. Since centrosomes are lacking, no asters are formed, but instead there appears at each pole of the nucleus a mass of clear material called a *polar cap*, in which fibers soon form. The cap increases in size, and as the nuclear membrane dissolves, a barrel-shaped spindle is organized. The remainder of the process differs little from what goes on in the lower plants; the chromosomes split at the equator and move to the poles, and two new nuclei are regenerated after which a cell wall cuts across the equator.

C. SUMMARY

From the abundant work done on karyokinesis, a few general conclusions may be derived.

1. The process probably effects an equivalent quantitative and qualitative distribution of the chromatin between the two daughter nuclei.

2. The chromosomes maintain their individuality through all the mitoses and only seem to disappear because vacuolized and converted into nets in the periods between divisions.

3. The chromosomes are the probable bearers of hereditary features: they constitute the germ-plasm.

4. Except for certain special cases, all organisms possess a definite and constant number of chromosomes in their nuclei. A few examples based on definite counts will be of interest. *Triticum vulgare*, the wheat plant, has sixteen (Overton, 1893); *Lilium tigrinum* has twenty-four (Schaffner, 1897); *Trillium grandiflorum* has twelve (Atkinson, 1899); *Asclepias syriaca*, the milkweed, has twenty (Strasburger, 1901).

It must be evident to the student that any attempt to explain the complex phenomena of mitosis on a physico-chemical basis is premature and puerile. In 1900 Wilson remarked:

> "At present we can only admit that none of the conclusions thus far reached, whether by observation or by experiment, are more than the first naïve attempts to analyze a group of most complex phenomena of which we have little real understanding."

In 1924 the same author says:

> "A consideration of the energies at work in mitosis leads us into one of the most difficult and debatable fields of cytological inquiry; the admission must indeed be made that after forty years of investigation we have taken no more than the first steps toward a real solution of the problem."

In 1925 certain Russian biologists reported a most curious phenomenon connected with mitosis. It was discovered that plant tissue of which the nuclei were undergoing the mitotic process possessed the power of starting the same activity in another plant. And what is more remarkable still, a growing tadpole can stimulate mitosis in plant tissue. The investigators refer the phenomenon to "mitokinetic rays" sent out from the mitotic figures and claim not only to have measured the wave-length of the rays but also to have determined their penetrating power to some extent. This brings up many unanswerable questions: Is the centrosome with its peculiar fibrillar asters and con-

BOTANY - LABORATORY OUTLINES

1ST YEAR HONOUR SCIENCE

Laboratory Period No.22

HE FLOWER: (Cont'd.)

ollination and Growth of Pollen Tubes in Stigmatic and Stylar Tissues.

Material: Pollinated carpels of buttercup or other flowers, bulk stained for temporary mounts.
Purpose: To observe course of pollination and pollen tube development.
Procedure: Study under the low power objective and observe pollen grains on the stigma, some of which will have germinated, to penetrating the stigmatic and stylar tissue. Pollen tubes can be followed for some distance in the style (do not confuse with vascular bundles). The nuclear details of pollen tubes have been studied previously.

Make a drawing to illustrate your observations.

The Morphology and Structure of a Monocotyledonous Flower.

$* \ \overbrace{K_3 \ C_3}^{P_{3+3}} \ S_{3+3} \ C_{\textcircled{3}}$

Sessile.

1. Material: Tulip or other flowers of the Liliaceae.
Purpose: To study the parts of the flower and their structure; to compare this flower with buttercup.
Procedure: (As for buttercup). Identify the parts of the flower noting: (a) the peduncle and receptacle; (b) calyx; (c) corolla; (d) androecium of stamens and their parts; (e) gynoecium. Of what parts and of how many whorls does each consist? On the basis of the stigmas, how many carpels have fused to form the compound pistil? Confirm this in part 2, after completing the initial study of the flower.

When as in tulip both calyx and corolla are similar, the whorls (two) together are called a perianth.

For convenience in drawing, one or more of the perianth lobes should be removed. Make a drawing (x2-3) labelling the individual organs and showing their attachment to the receptacle.

NOTE: In plants subjected to horticultural propogation and selection, floral modifications may occur. Look for irregularities in the numbers of parts in a whorl, especially in the gynoecium and androecium, for petaloid stamens and for other peculiarities.

Laboratory Period No.22

2. Make a cross section of the tulip ovary and examine under low magnification. Observe the three locules each of which contains a double row of ovules. Such a section together with the stigma lobes and the vascularization of the ovary lobes reveals the number of carpels which have fused to form the ovary of the pistil.

1 bundle/carpel

List the features of tulip which differ from those of buttercup.

Tulip more specialized.
① Redⁿ of # of parts -
② Parts in 3's & 6's instead of 5's.
③ Carpels fused
④ Perianth

3. The Structure of Lilium Flower.

Material: Transverse Sections of lily flower buds.
Purpose: To study the structure and the relation of the various flower parts.
Procedure: Study section under low power of microscope and observe (a) relation of perianth parts; (b) arrangement and structure of anthers; and (c) structure of ovary and ovules.

Each locule has 2 ovules -

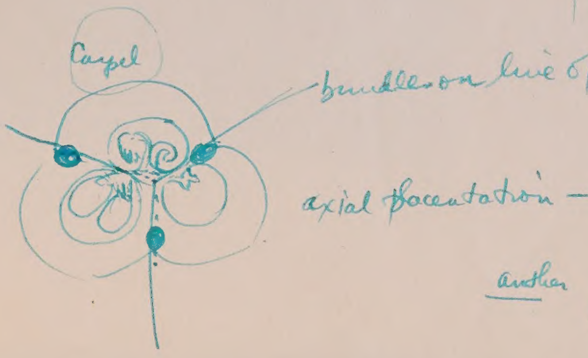
In anther observe lobes (thecae) and connective with vascular bundle (the filament is also shown in cross section in some of the slides). In each theca note integument of several cell layers, tapetal layer and pollen grains.

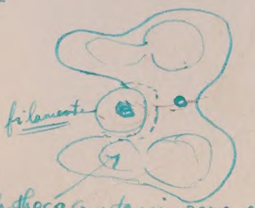
NB lines of fusion

In ovary, note locules and anatropous ovules, the latter showing funiculus or stalk and consisting of integuments with micropyle, nucellus and megaspore mother cell.

Epidermis
Fibrous layer
middle layer
Tapetum
anther

Make a diagram illustrating above features.





Each theca contains

Steiger - 6

Gore - 7

necting spindle concerned with this discharge of energy? Have these rays anything to do with "life"?

65. *Cellular Differentiation and Physiological Specialization*

Up to this point we have tried to confine our attention to an ideal cell, one in which structural features and physiological activities are seen in their simplest expressions. Yet from time to time it has been necessary to suggest the important fact which forms the topical basis for this paragraph. Cells are not all alike but vary remarkably in form, and the forms adapt them to the special activities which they must perform.

All plants begin their ontogeny as a single cell. Division after division goes on until the millions of cells of which the adult plant body is composed have arisen from the one. At first all alike, the cells become differentiated as they mature. Some become elongate and develop woody walls which the protoplasm sculptures with special pits; then they die and serve for water conduction. Others remain thin-walled and serve for food storage; others again lengthen out remarkably, thicken their walls, and turn into slender, strengthening fibers. Hence there comes into existence a plant body — a many in one — whose differentiated cells contribute to the general good.

66. *Summary*

Thus we reach the end of our introductory study of the cell, for when it has split into two parts we are on the threshold of another science, that of histology, the province of which is the study of cells in the forms of their aggregations into tissues. But before we step into this field, let us review briefly the material of the last chapters.

We have come to realize that the bodies of all living things are composed of building blocks called cells or protoplasts. Not only are cells the units of structure, but functions too find their simplest expressions in them. They are composed of a living jelly, protoplasm, which is differentiated into cytoplasm and nucleoplasm. Searching into the intimate structure of this "physical basis of life" with the help of physics and chemistry, we find it to be an extremely complex mixture of colloidal proteids with an addition of fats, carbohydrates, and other metaplasm. Included in it are also vacuoles, chondriosomes, plastids, sometimes a centrosome, and most important of all, a nucleus. The last is a complicated body containing nuclear sap, enzymes, linin, chromatin, and nucleoli. Chromatin, supposed to be the germ-plasm, has been chemically analyzed into a basic compound, protamine, specifically distinct for each kind of organism, and the protamine is combined with nucleic acid. Plant cells are surrounded by walls, primarily of cellulose, but often modified into other compounds. The wall is perforated by pits and is sometimes elaborately stiffened with spirals, rings, or bars.

Turning next to the activities of the cell, we find that its absorption of water and salts involves the physical principle of osmosis, though we realize that the living cell membrane introduces complications into the purely physical process. The study of metabolism familiarizes us with the essential activities which we consider as attributes of living things. We understand that anabolism leads to the constructive synthesis of protoplasm and the storage of energy, while katabolism accompanied by respiration involves the destruction of protoplasm with the release of energy. Energy so released manifests itself in physical changes, the most conspicuous being movements called tropisms, which are usually of an adaptive character.

The goal of the well-nourished cell is reproduction, and with a study of the complicated process of mitosis and subsequent cellular differentiation, our introduction to cytology is completed.

67. *Living versus Lifeless Matter*

It must have been noted in the preceding discussion of the cell that, though we have admitted without question the complexity of the structural and functional problems, we have attempted to place the interpretation of cellular activities purely on the basis of chemistry and physics. Still we have often used the terms *living cell*, *living membrane*, *vital phenomena*. Just what do such terms mean? Do biologists find evidence of any special kind of energy which they must call "vital force" or "life energy"? Is there any difference, except in degree, between inanimate and animate matter?

Let us first face the question as to whether there is any character or group of characters which will distinguish a living thing from a non-living thing. To put the problem in form, we will run back over the properties of protoplasm and see if there are phenomena in the non-living world which will simulate them.

1. Protoplasm seems to be a colloidal sol or gel. This certainly does not distinguish it from non-living glue, gelatin or mayonnaise dressing. It is more complex — that is all.

2. Protoplasm is an elaborate mixture of organic compounds largely proteidal, and contains much water. But here again there is no fundamental distinction, for any chemist can put together a complex mixture of organic compounds in water.

3. Protoplasm is very labile; its molecules are constantly changing. Here at first sight there seems to be a distinction from inanimate matter. Suppose a jellyfish and a steamer are both wrecked on the

seashore. The jellyfish compounds break up in a few hours; the steamer compounds lie decaying and rusting for perhaps a century. These are of course extreme cases, but they can be matched by their opposites. Flesh can be kept almost indefinitely in cold storage, while certain organic chemical compounds break up spontaneously in a few minutes after their formation. Hence, stability or instability of their chemical constituents does not differentiate dead from living matter.

So far as structure goes, then, we discover nothing which will fundamentally separate protoplasm from non-protoplasm. It is usually, however, by their activities that we know living things. Let us see if in the world of physiology there can be found some essential difference.

4. We must throw out the phenomena of osmosis and turgor, since our physical experiments demonstrated that the dead membrane possesses the same properties as the living one.

5. In the phenomena of metabolism and growth, if anywhere, we feel that a distinction ought to exist, and yet, strange as it may seem, the chemist can construct certain "chemical seeds" which will grow and carry on a simple metabolism. If a bit of copper sulphate, and water to cause it to granulate, is planted in an aqueous solution containing 2–4 per cent potassium ferrocyanide, 1–10 per cent of sodium chloride and other salts, and 1–4 per cent of gelatin, the "seed" germinates in a few hours to a few days. The copper sulphate reacts with the potassium ferrocyanide to form a membrane of cuprous ferrocyanide which behaves like any osmotic membrane, and the whole vesicle begins to grow. If turgor pressure ruptures the sac, the drop of exuded liquid is directly filmed over with a membrane. Such growths may come to be several inches high and may curiously simulate certain low forms of plant life. The student must not be swept off his feet by these facts. Such osmotic growths are not living plants; they are made of raw inorganic chemicals. Yet they certainly do exhibit features which were once held to characterize living things only. Mac Farlane says:

> "These are the necessary stages and phenomena that carry us from inorganic colloids with complex molecular composition and a high degree of intra-molecular energy to the varied series of organic colloids in which a still higher or biotic energy resides. Each osmotic growth has an evolutionary existence; it is nourished by osmosis and intussusception; it exercises a selective choice on the substances offered to it; it changes the chemical constitution of its nutriment before assimilating it. Like a living thing, it ejects into its environment the waste products of its functions. Moreover it grows, develops structures like those of living organisms, and it is sensitive to many exterior changes which influence its form and development. But these very phenomena — nutrition, assimilation, sensibility, growth and organization — are generally asserted to be the sole characteristics of life."

6. If the phenomena of metabolism and growth fail us, suppose we turn to the next property of protoplasm. Surely irritability is a phenomenon of living matter alone. Irritability we defined as the property which protoplasm possesses of reacting to stimuli. Yet a moment's thought teaches us that non-living things react to stimuli in a similar manner.

Since we used examples based on the influence of light when we were discussing protoplasm, let us confine our attention to the same form of physical energy now.

It has been known for some time that when light falls on the mineral selenite, electric currents are set up. Some years ago an ingenious physicist constructed the "selenite dog." This is an apparatus which is essentially a box with two selenite eyes, a motor inside and wheels beneath. When light falls on the "eyes," a current is generated; through the motor it is relayed to the wheels, which begin to turn. If I go out at night with a lighted lantern, the "dog" will follow down the street; if I turn a corner, the "dog" also turns. As I turn, one of the selenite "eyes" is receiving stronger illumination than the other. Hence that eye is generating a stronger current, and the wheels are so wired that those on the outside circumference of the turn receive the stronger stimulus.

The selenite "dog" is no more remarkable than the strange boats which can be guided through the water by wireless waves.

Let us now turn back to a new interpretation of the green phototropic flagellate. Light falls on the protoplasm; certain light-sensitive chemical compounds are decomposed (even as on a photographic plate), and energy is released and conducted to the flagellum; active rhythmic contraction is set up, the flagellum moves, and the small plant cell is whipped forward into the light.

Suppose we apply the same line of reasoning to an animal. A moth flies into a room in which burns a candle and hurls itself into the flame. We may say that the pigment of the retina of the eye undergoes a chemical change due to the entering light. Energy is released; it sweeps through the optic nerve to the brain ganglia, is relayed through chains of neurons along the nerve cord to the muscles of the wings; the muscles contract, the wings beat, and the moth is propelled into the flame. Many times, however, such insects fly about the flame without entering it. We may realize that our selenite "dog" would behave in the same erratic manner if it possessed wings and if its eyes were unequally lighted, for one wing would beat faster than the other. Thus irritability fails us as a feature of distinction between the animate and the inanimate world.

7. Another function of living things is reproduction. This need

not detain us when we realize that simple reproduction is only a kind of division and that from osmotic growths certain portions will often break off and start new growths.

8. A last activity, which has been called a directing principle of organization, is sometimes held to characterize organisms, at least those of higher types. For example, we see that root, stem, leaf, and flower are not separate parts of a plant, each carrying on its activities independently, but that they are bound into a harmonious and coöperating system. It has been discovered that this harmony depends, in part at least, upon *chemical regulators* which migrate from one part to another and control the physiological activities. We all know that when a terminal shoot of a tree is removed, the lateral buds begin to develop to take the place of the lost member. This looks like a conscious or intuitive attempt to restore harmony. Actually it has been proved, in some cases at least, that the terminal bud secretes certain substances which drift backward along the twig and inhibit the growth of the laterals. When the terminal bud is destroyed, the inhibition is removed.

So we come to the conclusion, which intellectual honesty forces us to face, that so far as science can go there is no special property or set of properties which separate the non-living from the living world. As Leduc says:

> "Considering the impossibility of defining the exact line of demarcation between animate and inanimate matter, it is astonishing to find so much stress laid on the supposed fundamental difference between vital and non-vital phenomena. There is in fact no sharp division, no precise limit where inanimate nature ends and life begins. The transition is gradual and insensible."

68. *Mechanism versus Vitalism*

At first glance the above conclusion seems to dispose once for all of the life problem and reduces us to a position where we must believe that chemistry and physics will ultimately resolve the phenomena of life into complex motions just as they do the phenomena of non-living matter. There are biologists who believe this. In their opinion biology is merely an extension of physics and chemistry, and they hold that a sufficiently perfected science will ultimately be able to manufacture protoplasm in the laboratory and duplicate all the phenomena of life. Such men are called *mechanists*.

On the contrary there are biologists who believe that living things are really "alive" — that they are chemico-physical machines plus a something else which they call a vital force or life principle. These biologists are called *vitalists*. They hold that a metaphysical factor enters into the problem of life, and that the life principle, since it is supersensuous, eludes the scientific grasp and can never become a subject for scientific investigation. A quotation from a prominent vitalist * will make their view clearer:

> "Life is neither matter nor energy, nor even a function of matter or of energy, but is something belonging to a different category; it is dependent on matter for its phenomenal appearance, but otherwise I conceive that it is independent, that its essential existence is continuous and permanent, though its actions with matter are discontinuous and temporary; and I conjecture that it is subject to the law of evolution — that a linear advance is open to it whether it be in its phenomenal or in its occult state."

69. *The Life and Death of Organisms*

Organic death ensues when the power which propelled the machine is turned off. Whatever metaphysical view of death we may take, in actual fact we know well enough what is meant by a dead as opposed to a living organism, and so we may ask the question: Can we distinguish whether a body once living is still alive? Suppose one gives the student a grain of wheat and asks him whether it is living or dead. It might conceivably be too far gone to germinate. A certain delicate chemical test would practically settle the matter. It will be remembered that we said that protoplasm respires all the time; every living thing is evolving carbon dioxide. Hence, if a delicate enough test for the gas can be devised, we ought to be able to decide the question. Such an apparatus has been made. It consists essentially of a chamber inside which the seed or other body is placed. The original gases in the chamber are displaced by some inert gas. Along with the body to be tested is a tube of fresh barium hydroxide solution. The whole is carefully sealed. If carbon dioxide is evolved from the seed by the process of intramolecular respiration which goes on in the absence of free external oxygen, it will produce a trace of insoluble barium carbonate on the baryta water and this may be searched for with the compound microscope. If found, it means that the body is alive. We may think that we have here an absolute test for life, and yet if we take a handful of wheat and place it in liquid air (boiling point, $-194°$ C.), all evolution of carbon dioxide ceases necessarily, since the gas becomes a solid at such a temperature. It might be said that the seeds had been killed by the intense cold, but let us remove the same seeds and plant them; they will germinate, showing that they were not dead. Or if they were "dead" while in the liquid air, they came to "life" again later. Does not this tend to substantiate the conclusion which we have already reached that the protoplasmic system is a machine whose activities can be inhibited by cold in a manner analogous to the way a clock

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* Sir Oliver Lodge.

"freezes up" in cold weather due to the thickening of the oil in its works?

Of course the carbon dioxide test only tells us with near approach to truth whether an organism is still living (or at least respiring). It does not distinguish between inorganic and organic bodies. Let hydrochloric acid act upon marble and we could get an excellent "test for life," for carbon dioxide would be given off here too.

The cells of both plants and animals possess a life which is distinct from the general life of the organism itself. This is particularly evident in plants, for if their bodies are cut into fragments, the separated cell masses will regenerate the whole plant. The lower animals possess the same property. If a hydra is cut into pieces, each fragment can regenerate a new hydra. Even embryonic human flesh can be grown indefinitely as small amorphous masses in glass jars of culture solutions.

70. *The Origin of Living Things*

Do living things to-day ever arise from a source which is not living? In other words, does spontaneous generation or abiogenesis ever take place? For many years this question was a point of acrimonious dispute among biologists, but it has been settled for the present at least. We have no accepted scientific evidence that living things ever arise from a non-living source. All life comes from preëxisting life: *Omne vivum ex vivo.*

It is interesting to turn back the pages of history and see what the men who came before us thought about the origin of living things. There was a popular belief among the Egyptians that mice and frogs were generated from the mud of the Nile. Virgil tells us a story about bees spontaneously produced from a dead bullock. In the Middle Ages there was a famous recipe for generating mice: Place old rags and corn in a jar; set it aside for a time and mice will spontaneously appear there. Milton gives us spontaneous generation with a vengeance in his realistic description of how lions arose from the dust of the earth.

> "The grassy clods now calved; now half appears
> The tawny lion, pawing to get free
> His hinder parts — then springs as broke from bonds
> And rampant shakes his brindled mane."
>
> *Paradise Lost*, Book VII.

It was not till 1680 that the first stones were thrown into the camp of the spontaneous generation school. It was generally believed that maggots arose spontaneously in decaying meat. Redi, an Italian, easily disproved this by screening the meat from flies. The defenders of the spontaneous generation theory were soon forced to abandon their beliefs as far as the higher organisms go, but they wisely retreated from this exposed front and took up their position in the realm of microscopic life, where they put up a hot fight. It was discovered that microscopic organisms would spring up even in boiled and stoppered nutrient solutions. We realize to-day that the reasons for this lay in the fact that the early biologists were not aware that certain bacteria in a special resting condition, which we call the spore state, can stand the temperature of boiling water; furthermore, they did not sufficiently appreciate the ease with which sterilized solutions are contaminated by dust from the air.

The question as to the possibility of spontaneous generation was finally settled in the negative by the labors of many men such as Spallanzani (1777), Pasteur, and Tyndall. To test the theory Tyndall devised an ingenious experiment that is worth describing. He constructed a dust-proof box with small windows on two sides and also a glass front (Fig. 97). The inside of the box was coated with glycerin to catch any dust particles which might be present to begin with. In the bottom of the box was inserted a plate pierced with holes through each of which was sunken a test tube so that most of its length hung below the box, but its mouth was open to the dust-free atmosphere inside. In the top of the box were inserted glass tubes bent into several loops and coated inside with glycerin. These were for the admission of air, since the spontaneous generationists had argued that air was necessary to initiate life. So Tyndall permitted the air to enter freely, but no dust ever passed beyond the second loop of the tubes. Through the top of the box was also thrust a thistle tube which penetrated a rubber diaphragm. This was to permit one to pour materials into the test tubes inside. He now set the apparatus aside and waited till a ray of light passing through the box between the windows was no longer visible. This meant that all the dust had been caught on the glycerin-covered walls. Then he filled the test tubes with various sorts of good "spontaneous generation media," such as cheese, beef broth, etc., and last of all he plunged the free bases of the test tubes into boiling oil to destroy any living thing which might be present. He now had tubes of sterile material opening into a dust-free atmosphere, and he set his box aside

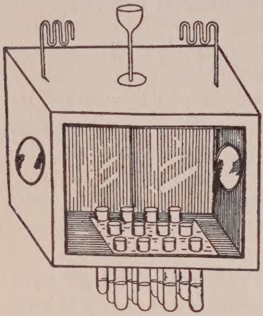

FIG. 97. — The "Tyndall Apparatus" Whereby Spontaneous Generation Was Definitely Disproved.

to watch developments. Result: the solutions remained indefinitely unchanged, and no living thing ever appeared in them.

Well, if living things to-day only come from preceding living things, where did the first ones come from? Geology and astronomy teach that there was a time when the earth was without any living organisms. Then, if this be so, there must have been a definite beginning. Several partial answers may be given to the question just propounded. The Swedish physicist Arrhenius has suggested that the original germs of life may have come from another planet, borne by waves of light. We suspect that there may be living particles small enough to be transported in this way, and we suspect, furthermore, that the cold of interstellar space would not destroy them, since if bacteria can withstand the temperature of liquid air, they would seem to be able to withstand almost any degree of cold.

Another solution of the problem is to postulate a primal spontaneous generation. We have seen already that certain colloidal growths suggest that there are intermediate steps between inanimate and animate matter. The following quotation from Mac Farlane is at least suggestive if no more:

> "Living substance very gradually originated among chemically acting and reacting inorganic compounds in aquatic situations and where colloid as well as crystalloid bodies tended to arise through environal agency. From long continued interaction of emulsoid and suspensoid types of colloid compounds, a chemically sensitive and yet stable mixture of several colloids resulted, that we now call protoplasm."

Though no biologist has seen such growths arising in a state of nature, yet he can deny neither that they once did so arise or that they may not even now be coming into existence — perhaps in tropical seas or in hot springs. It is in the latter situation to-day that a group of the most primitive of existing plants make their home.

In addition to this there is a biological mystery which may possibly bear upon the subject. For some years it has been known that certain infectious diseases (e.g., Texas fever of cattle or influenza) cannot be linked up with any visible causal "germ." Liquids from organisms suffering from the disease can be passed through porcelain filters, and yet when injected into healthy organisms the filtrate will provoke the disease. Such disease-producing liquids are called "filtrable viruses." The question at once arises: Are there organisms (bacteria or protozoa) in these viruses so tiny that no microscope can detect them, and which are able to pass through the pores of a porcelain filter? Or are these hypothetical particles semi-living stages arising from "dead matter" and transitional to true protoplasm? If so, we must abandon our dictum: *Omne vivum ex vivo*. Or, last of all, are they dead particles?

Be they dead or living, if they arise *de novo* and under unknown conditions, then the problem of the control of public health assumes a decidedly serious aspect. We have laughed at the ideas of the ancients that epidemics could be due to "miasmas" rising from swamps, or to exhalations from tombs. Shall we have to admit, perhaps, that they had an inkling of the truth?

We have now laid a biological foundation on which we shall proceed to erect a structure of purely botanical matter. It will be recalled that after a résumé of the cell some pages back, the statement was made that with cell-division we are on the threshold of another science, that of *plant histology*, which deals with the details of tissue structure. We shall now step over the threshold.

CHAPTER XII

ANATOMY OF THE VEGETATIVE SYSTEM OF THE SEED PLANTS

71. *The Phylogenesis of Tissues*

We have reason to believe that at one time, ages ago, the earth's whole flora and fauna consisted of unicellular organisms which swarmed in the ocean. In those days, so geology tells us, the lands were but barren lava fields or heaps of sand and gravel laid down by the rivers. But in the sea, warmed and lighted by the sun, filled with dissolved food salts and gases, conditions were quite as favorable for the development of organisms as at present.

The sea is still the home of the descendants of this primal, microscopic swarm of unicellular life. It drifts about in the surface waters of all the oceans and constitutes a part of the *plankton*. Not only is it of great theoretical importance, since it forms the roots of the phylogenetic tree of both plants and animals, but in addition, it is the basis of the dietary of sea animals and its small plants form a link in the nitrogen cycle, since they pick up the nitrogenous wastes swept from the land and synthesize them into proteids. They become the food of small crustacea, molluscs, worms, etc., which in their turn are preyed upon by fishes which enter into the dietary of man.

The simplest members of the phytoplanktonic swarm are unicellular organisms — green flagellates like *Euglena*, minute bacteria, diatoms with skeletons of transparent glass, whirling dinoflagellates, fire globes of *Pyrocystis* (the plant which is responsible for the brilliant phosphorescence of the tropical seas).

The method of reproduction of most of these unicells is very simple: the nucleus divides by mitosis, and the mother cell separates into two daughter cells which become the independent parents of a new generation.

Let us follow briefly the theoretical course of such organisms as they evolved into higher types. The time came when the daughters resulting from a division, or from repeated divisions, did not separate but remained coherent instead to form a multicellular mass. This was the first tissue: a collection of similar cells bound together and doing a similar work. Probably at first the aggregation was merely mechanical, but as ages passed a curious change came about: the mass began to act as a unit and became an organism. Such simple organisms still exist; an example is *Pandorina* — a swimming colony of sixteen cells imbedded in jelly. Another is *Volvox*, a hollow ball of numerous chlorophyll-bearing cells which are obviously integrated into a unit, since the ball swims with a certain pole always in advance and there is some division of labor among the cells. *Volvox*, however, in spite of its green color, is more like an animal than a plant. Its body is similar to the blastula, a stage through which our own embryo passes in its ontogeny.

In the more specific plant line, the successive division walls of the primal unicell tended to lie parallel to one another, with the natural result that a filament analogous to that of *Spirogyra* (Fig. 88) came into being. Subsequent divisions in the other two planes of space slowly evolved bulkier tissues. In this primary plant tissue certain brigades of cells were worked over through evolution to do special kinds of work. Hence arose protective tissue, supportive tissue, conductive tissue, and so on, which were later in their turn aggregated into systems or into organs such as root, stem, and leaf.

In conformity with the recapitulatory law it will be evident that the individual ontogeny follows the same sequence of development as that just outlined. The human body, for example, starts with a single cell. This cell expands into a simple tissue (blastoderm); then it differentiates into several tissues (ectoderm, endoderm, mesoderm — and later into skin, bone, muscle, and other parts) which are assembled into organs (heart, brain, stomach, lungs) and linked up into systems (respiratory, nervous, digestive, circulatory).

At this point we may bring up a subtle problem. What is an individual? Was the original cell which lived in the ancient sea an individual? Is the *Pandorina* colony, which arose both phylogenetically and ontogenetically from the unicell, one or sixteen individuals? Or, to push the problem to the extreme: Is a man one or some millions of individuals? Is my "I" the fusion product of many cellular psychic "I's" whose coöperative society makes up my body? If this be so, whence is the sense of unity derived?

On the other hand, if the cells arising from a parent cell do not remain together but disperse widely, as they do, for example, in *Euglena* or *Amœba*, what becomes of the individuality of the parent, and would the collection be one or many organisms? Is physical contiguity necessary to individuation? May it be that there is only *one Euglena viridis* in all the waters of the world? To push this question likewise to the extreme: What is the "spirit of the hive" to which instinctual bees and ants are subordinated? What is a flock of birds, a school of fish (or of students)? What is MANKIND?

In all these questions we are touching upon the mystery of relativity of consciousness and of individuality. We can see a mathematical analogy to our biological problem, in the relation of line to square, of square to cube, of cube to tessaract — that hyper-spatial solid which (to us) extends into time.

72. *The Tissues of the Plant Body*

Having seen how tissues originated in phylogeny (and their ontogenetic sequence is strictly parallel), we must now engage upon a somewhat technical study of the tissues which we find in the bodies of flowering plants. The following pages will demand courage and close application — thus only does one climb mountains. Perhaps at the end we may find that we have come to a new plateau of thought where we will be rewarded by another "long view."

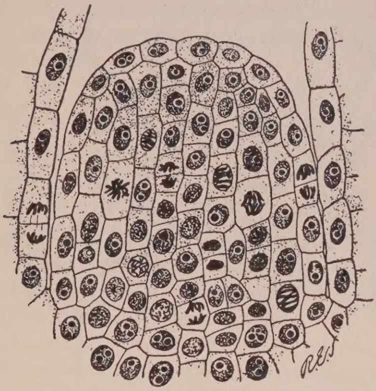

FIG. 98. — Meristematic or Formative Tissue. The oval mass is a longisection of the plumular leaf of an onion seedling. It is still enclosed by the cotyledonary sheath.

A *tissue* may be defined as a collection of similar cells doing a similar work. Plant tissues are distinguished from one another by the shape, contents, wall thickness, and functions of the constituent cells. The science of tissues is called *histology*. The following classification is based upon the functions of the various plant tissues.

To begin with, all tissues may be divided into (A) meristematic or formative, and (B) permanent, tissues.

A. MERISTEMATIC OR FORMATIVE TISSUES

All plants in their embryonic stages, or all plant parts in their initial condition, such, for example, as young root and stem tips, young leaves in the bud, etc., consist of a tissue whose cells are in process of rapid division and growth. Moreover, they are full of cytoplasm, have no conspicuous vacuoles, and possess large nuclei. In thin, stained sections they are often found full of karyokinetic figures. Such a tissue is called *formative* or *meristematic tissue* (Fig. 98).

If one were provided with microscopic vision to follow these cells day by day as the plant developed toward maturity, one would see them pass through stages of differentiation till they finally became adult wood cells or pith cells or cork cells. Such adult tissues which arise directly from the meristems of embryos or from growing tips of twigs, roots, and the like are called *primary tissues*, and the meristems from which they arise are known as *primary meristems*. Those primary meristems which occur at the apex of roots and stems are called *apical meristems*.

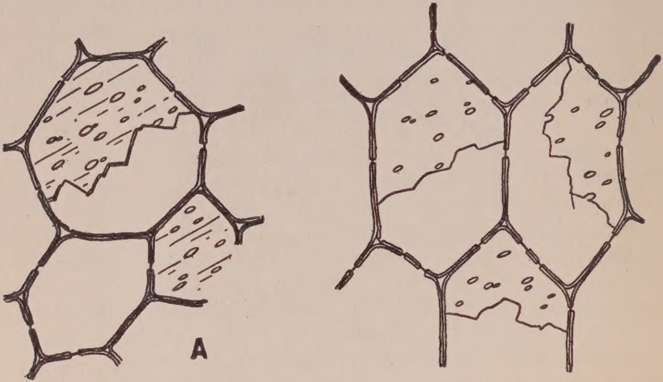

FIG. 99. — Cross-Section and Longisection of Elder-Pith Parenchyma. Both sectional and surface views of the cell walls and their pits are shown.

The term *secondary*, as opposed to primary, is applied to tissues which arise from what are termed *secondary meristems*. A secondary meristem is a dividing and growing tissue which starts up from cells which have already attained their adult condition; its origin is a kind of rejuvenescence. We have all seen a wound on a tree healed by an overgrowth of *callus tissue*. The callus is a secondary tissue which arises from a secondary meristem. Certain of the bark cells which receive the wound stimulus become meristematic and lay down the healing callus. The true *cambium* which forms the annual rings of wood and phloëm, and the *cork cambium* which thickens the bark, are also secondary meristems. Hence the tree possesses both primary wood and bark (derived from the primary meristems) and secondary wood and bark. The former is relatively trifling in amount in modern trees, though in archaic woody types it constituted the main bulk of the plant.

B. THE PERMANENT OR ADULT TISSUES

There are several kinds of permanent or adult tissues in a plant. They may be classified according to the work they do as (1) parenchyma or fundamental tissue, (2) boundary tissues, (3) mechanical tissues, and (4) conducting tissues.

(1) *Parenchyma or Fundamental Tissue.*

Parenchyma is a basic, general-purpose tissue which does a great variety of work; hence it can hardly be defined on a basis of function. Morphologically, we may say that its constituent cells contain protoplasm and have thin walls of cellulose provided with simple pits. In Fig. 99, A and B, are seen cross and longitudinal sections of the dead parenchyma of elder-pith. In parenchyma foods are synthesized, and it also stores food and water; it serves incidentally as a packing material around other tissues; it secretes and conducts. Certain special types have received special names. *Chlorenchyma* is a manufacturing parenchyma whose cells contain chloroplasts; *aërenchyma* is a sort of respiratory or aërating tissue and conducts air into the plant; it is well developed in the "knees" or pneumatophores of the bald cypress (*Taxodium*). *Secretory parenchyma* discharges certain useful chemical substances; the nectaries of flowers belong to this category, and their parenchyma secretes sugary solutions to attract insects. The glandular cells which line the cups of the pitcher-plant secrete proteolytic enzymes to effect the digestion of drowned insects.

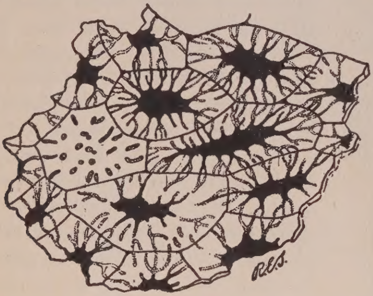

FIG. 100. — Section of Peach-Stone Sclerenchyma. The extreme thickening of the cell walls has reduced the cell cavities and converted the pits into tiny and often branching tunnels. In a cell at the left the knife has failed to cut into the cavity.

(2) *Boundary Tissues.*

Boundary tissues, as the name suggests, mark off or bound certain other tissues. The *epidermis*, or often the *cork tissue*, bounds the cortex exteriorly, while the *endodermis* delimits the same layer from the deeper-lying tissues inside it.

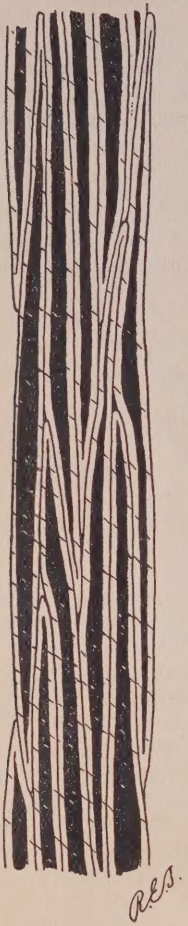

Fig. 101. — Sclerenchymatous Fibers from the Outer Rind of a Cornstalk. The pits are tiny and slit-like.

(3) *Mechanical Tissues.*

The body of a plant is often subjected to great strains; gales of wind test it severely, ice and snow may load its branches, and even the weight of foliage, flowers, or fruit may produce high tensile stresses. To counteract such tendencies to deformation and breaking, special tissues are developed. *Sclerenchyma* is one of these. The word itself means "hard tissue" and is applied to a tissue whose cells have thickened walls. They are commonly dead and given over purely to the function of protection and support. Fig. 100 represents the sclerenchyma of the peach-stone. Some sclerenchyma cells are long and slender, tapering at both ends, and these are called *fibers* (Fig. 101); others almost isodiametric, like tiny sand-grains, are sometimes called *stone cells*. They occur in the flesh of the pear near the core, and their gritty, disagreeable nature is well known. Some sclerenchyma cells have very irregular shapes; they may bear long horn-like processes and by matting together form protective sheets around more delicate structures.

Collenchyma (Fig. 102), is a tissue whose constituent cells are shaped much like those of parenchyma, except for the fact that they are thickened at their corners or on one face. They contain protoplasm. The function of collenchyma is that of a strengthening tissue, but it is more flexible and elastic than is sclerenchyma and is capable of growth, since the cells are living. It is analogous to cartilage in the animal body.

(4) *Conducting Tissues.*

Our plant can now stand erect; it can manufacture and store food; it has a skeleton of mechanical tissue; it is protected by boundary tissues. But as yet we have given it no method of conducting liquids and foods rapidly and efficiently through its body. Such a system is supplied by the *conducting tissues*, which constitute the most complex part of the plant. They will be considered in detail later when we come to the study of stem anatomy.

(5) *The Stele.*

The various kinds of tissues just characterized are associated in seed plants in two tissue systems known as the *stelar* and the *extra-stelar systems*. The Greek word *stele* means "a column" and is applied in morphology to all the structures of the stem of one of the higher plants which lie inside the endodermis, the endodermis being the boundary tissue which shuts off the stele from the cortex and epidermis. The subject of comparative stelar morphology is one of the most fascinating of botanical studies, the reason being that in its progressive evolution the stele offers us one of the most remarkable documents for the truth of the theory of evolution that we possess. Not only can we follow a striking series of stelar types from ferns through gymnosperms to angiosperms, but since the stele is largely composed of wood, it is easily preserved in fossil form, with the result that the record of stelar evolution can actually be traced back through a period of approximately 400,000,000 years to the ancient Devonian Period.

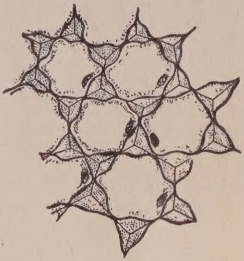

Fig. 102. — Collenchyma from the Superficial Part of a Begonia Petiole.

So we get an initial glimpse into the structure of the vegetative system of the flowering plant. Composed of millions of cells, each kind gathered into tissues which arise from either primary or secondary meristems, the tissues associated into organs and the organs merged into two great systems — vegetative and reproductive. All are members of one body and coöperating for its good.

We shall now take up the study of two stems, considering their various tissues in some detail. These two stems will be those of the pine and the oak.

It will be remembered that the pine is one of the oldest living trees, and that through its ancestor *Prepinus* its history can be traced back to the Cretaceous Period. Its stem structure is relatively simple, and it will serve as an excellent basis for the interpretation of the more modern and more complex structure of the oak.

73. *The Anatomy of the Pine Stem*

It is evident that with the naked eye or with gross dissection we can learn very little about the structure of the pine stem; its tissues are too tightly bound together. Consequently it becomes necessary to cut thin sections, to stain them with various dyes, and then to study them under magnification. Even the simple lens reveals considerable structure (cf. Fig. 103 with the legend of Fig. 104); but under the compound microscope the histology is found to be very complex.

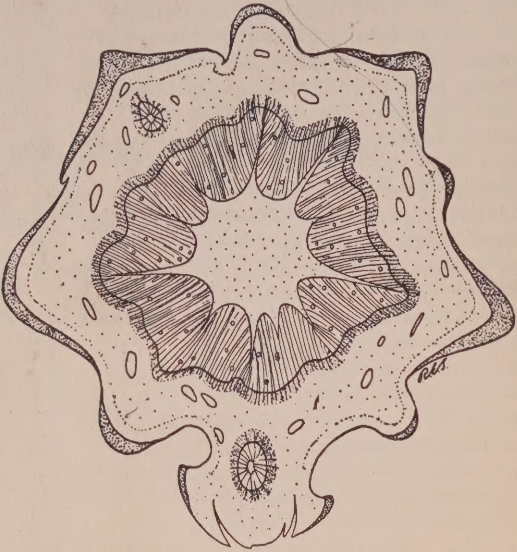

FIG. 103. — Diagram of Cross-Section of One-Year-Old Twig of the Austrian Pine (*Pinus austriaca*). Comparison with Fig. 104 will enable the student to identify the parts. The oval body imbedded in the cortex at the lower center is the section of a short-shoot.

If two stains have been used in the preparation, it will be observed that the central woody mass of the twig has taken one color, while the bark has taken another. In the center lies an area which stains like the bark. We learned when studying the cell that such differential staining is considered to be an index of difference in chemical composition. Cell walls of wood or lignin stain differently from those composed of cellulose. It should be realized, too, that we are dealing now with a cross-section of the twig and that the real three-dimensional shapes of the cells will not be understood till we come to study longitudinal sections.

The following rather detailed study will demand thorough laboratory work. Fig. 104 may be used for comparison.

A. EXTRA-STELAR TISSUES — EPIDERMIS, CORK, AND CORTEX

The twig is covered with an *epidermis*, a single sheet of boundary cells which is now seen cut in cross-section. In hard pines the epidermal cells and the next layer beneath (*hypodermis*) are often sclerenchymatous, as our figure shows. Beneath the hypodermal layer is a band of paler and often distorted tissue (*cork*) whose cells lie in files and grade away on their inner side into a layer of narrower and nucleated cells. This last layer is the *cork cambium* or *phellogen*, a secondary meristem which arises very early in almost all stems and proceeds by successive divisions to form a layer of cork on its outer side. The method through which cork originates is as follows: a cell of the cork cambium undergoes mitotic division, and the outer of the two resulting cells slowly thickens its walls with a substance known as *suberin*, and finally dies. The inner cell grows to adult size and divides again, and once more the outer cell is suberized and converted into cork. It will be evident that if the cork cambium is to continue cutting off new cells on its outer face, they must necessarily push outward and finally disrupt the epidermis. This is what actually does happen, and the epidermis very early becomes fissured and split.

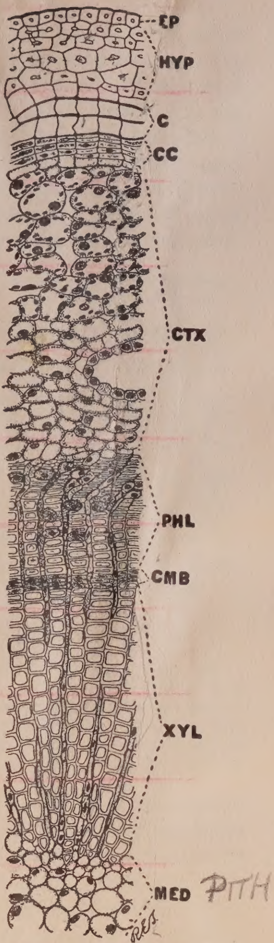

FIG. 104. — Magnified Portion of Fig. 103 Including the Tissues from Pith to Epidermis: EP, epidermis; HYP, hypodermis; C, cork or phellem; CC, Cork cambium or phellogen; CTX, cortex; PHL, phloëm; CMB, cambium; XYL, xylem or wood; MED, medulla or pith.

The first-formed layers of cork cells, however, abut against the resistant sclerenchyma of the hypodermis and consequently they are often crushed and distorted out of recognizable existence. Only later does the pressure which they exert suffice to disrupt both epidermis and hypodermis.

In addition to cutting off cork cells on its outside, the cork cambium often forms a thin layer of living tissue (*phelloderm*) on its inside. While in living trees the layer is usually of negligible importance, it played a striking part in ancient trees. All the secondary tissue produced in the cortex by the cork cambium is called *periderm* or *secondary cortex*. Fig. 105 shows a section of willow bark with epidermis and periderm.

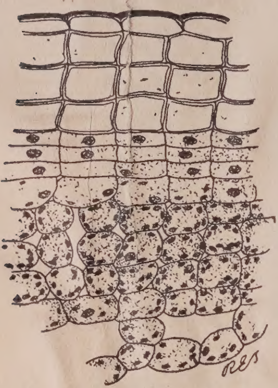

FIG. 105. — Section of Willow Bark Showing Epidermis, Cork, Cork Cambium, and Phelloderm. The last three tissues constitute collectively the periderm; it may also be called secondary cortex.

Cork cambium often starts to develop in small areas beneath the epidermis. This causes local fusiform splits to develop through the epidermis and under each of these splits the cork cambium forms a peculiar kind of aërenchyma. The whole apparatus then constitutes a *lenticel* and serves as a respiratory pore through which gases enter and leave the green cortex (Fig. 106). Lenticels often form conspicuous markings on many twigs.

In some cases cork cambium develops deep within the bark of the tree, and, since cork is impervious to water, all the cells outside of it die and may finally scale away in the form of flaky bark such as is so commonly seen in sycamores. On the other hand, a cork cambium may sometimes start in the epidermis. Hence it will be seen that a definition of the cork cambium must be based on its function rather than on its origin or position.

A brief summary will be useful here. Cork cambium (phellogen), a secondary meristem, may arise in epidermis, cortex, or in phloëm. It produces dead cork (*phellem*) on its outside and living phelloderm on its inside. All these secondary tissues constitute collectively the *periderm*, and if they arise, as is usually the case, in the cortex, they may be called secondary cortical tissues.

Returning to the study of the pine and of Fig. 104, we may note that under the cork cambium lies the *cortex* — essentially the *green* *bark.* It is a layer of parenchyma which contains chloroplasts and consequently offers us an example of that special parenchymatous tissue which has been called chlorenchyma. In sectional aspect the cells of the cortex vary from circular to elliptical; among them abundant intercellular spaces will be detected, through which in life air is always circulating. Distributed through the cortex lie several very conspicuous structures, each of which consists of a large space surrounded by a few layers of smaller and densely protoplasmic cells.

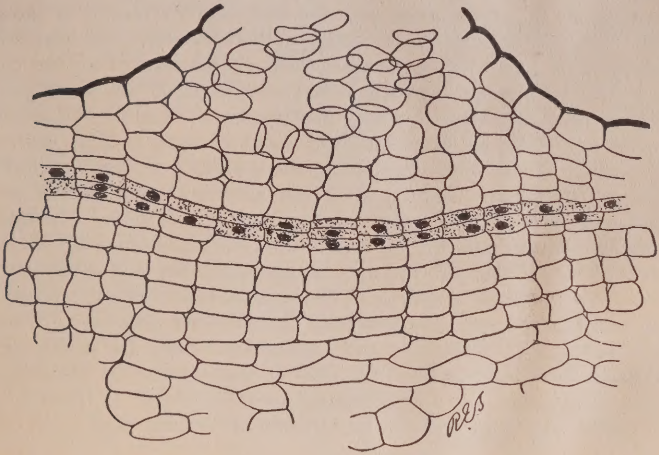

FIG. 106. — A Section of the Lenticel of the Elder (*Sambucus*). The cork cambium has produced aërenchyma (known technically as complementary tissue) on its outside, and the outward pressure has ruptured the epidermis. Beneath the cork cambium is a layer of phelloderm, while below this is seen a bit of the true cortex. Nuclei and cytoplasm are represented only in the cork cambium cells.

The student need only ask himself what oozes from a pine twig when freshly cut to realize that these are the sectional views of the *resin canals* through which pitch flows. The cells around the cavity belong to the category of secretory parenchyma; they synthesize the resin and pour it into the canal. Pine pitch is of considerable economic importance, since turpentine is derived from it. Strangely enough, too, the substance amber, used for jewelry and for small ornamental articles, is fossilized pitch. Along the Baltic Sea in the Oligocene Period grew forests of pines of a species called *Pinus succinifera* (succinite being the technical name for amber). Large quantities of their pitch has been found fossilized into amber and in some cases the masses contain most exquisitely preserved insects or leaves or small flowers. A little amber has been found in the same American Cretaceous beds from which *Prepinus* was derived.

B. STELAR TISSUES

(1) *The Phloëm.*

As we leave the cortex and pass still farther inward, a region appears composed of three sorts of tissue; this part of the stem constitutes the *phloëm* or *bast.* One of the cell types is small, narrow, and rectangular in cross-section, with the individuals arranged in radial files. The files are interrupted here and there by larger and oval cells which often have dark contents. Most conspicuous of all the cell types are the chains of radially elongated cells which can be followed inward till they penetrate deeply into the wood. The files of narrow rectangular cells are cross-sectional views of rows of *sieve cells,* a conductive tissue whose function is to transport metabolized foods through the plant. They receive their name from the curious perforated *sieve plates* which they bear on their lateral walls. The large oval cells which interrupt the files of sieve cells constitute the *phloëm parenchyma.* Their cells serve as storage reservoirs and usually contain more or less oil or starch. The chains of cells which run radially inward and penetrate the wood are the so-called *wood rays.* Their function is that of storage and conduction. They are living, and through them the wood and the phloëm keep up osmotic connection with one another. So the phloëm of the pine consists of these three elements: sieve cells, phloëm parenchyma, and wood rays.

(2) *The Cambium and Its Activity.*

The phloëm grades away on its inner border into a layer of cells which constitutes the *cambium.* The cambium is perhaps more easily detected if we realize that it lies right on the outer face of the wood. It is but a few cells in thickness, and since its thin walls are of cellulose, they take the same stain as do those of the phloëm or cortex. As seen in tranvserse section, cambium cells are narrowly rectangular; they lie in files and the wood and phloëm cells which they produce by repeated divisions also lie in files. Cambial cells are considerably elongated in the vertical direction; they might perhaps be compared in shape to short planks with tapering ends. The cambium layer, of which the layman in horticulture hears so much and really knows so little, is of extreme importance to the plant. It is a region of permanent meristem, and during the growing season its cells are ever undergoing division, to differentiate later into phloëm on the outside and new wood on the inside. It will be realized that if new phloëm is being produced, it must crowd the older phloëm outward to make a place for itself in a manner exactly similar to that in which cork crowds outward. This pressure becomes so intense that the final result is to crush and distort the older and outer phloëm and finally to rupture the outer tissues. It should also be understood that as new wood is formed on its inner face, the cambium is moved farther and farther from the center of the tree. In a young twig it lies only a few millimeters from the pith; in an old tree it lies at a distance of many decimeters from the center. As the tree increases in girth it is evident, too, that the cambium must increase the number of the radial files of its cells.

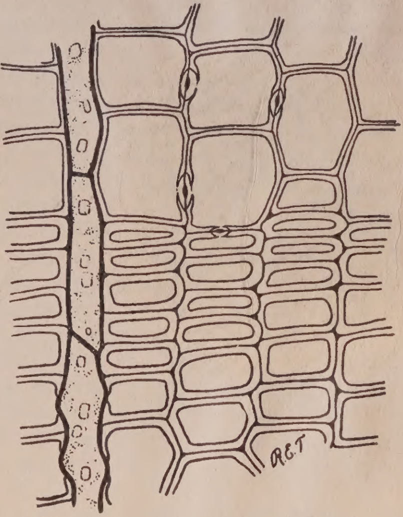

Fig. 107. — Small Portion of Pine Wood Seen in Cross-Section and Highly Magnified. Both spring and summer tracheids are represented. A wood ray with cellulose walls conventionalized in black is also shown. On the radial walls of several spring tracheids sections of bordered pits appear.

(3) *The Xylem or Wood.*

The region of the *wood* or *xylem* is known in its gross aspect to every one. In an old stem it is usually differentiated into two regions. On the outside lies the paler *sap-wood* which carries on practically all the work of conducting water and salts, while within there is an irregular area of non-functional *heart-wood*, often darker in color because of the resinous or tanniferous compounds found in its cells. The heart-wood has little use other than that of support, and though its antiseptic inclusions may inhibit decay for some time, yet as all are aware, it may eventually rot away completely with little seeming physiological detriment to the tree. Because of its freedom from moisture, its durability and its dark and often beautiful color, the heart-wood is the most valuable for choice cabinet work. Ebony, mahogany, and rosewood are all derived from the heart-wood of their respective trees.

If we now continue the microscopic study of the pine twig, we see that the wood consists of thick-walled, angular cells lying in radial files and that these cells alternate and more or less dovetail with one another. (Fig. 107 shows this region under high magnification.) Let us remember that this is a cross-section. The wood cells, which take the special name of *tracheids*, are actually elongated and more or less hexagonal prisms pointed and interlocked at both ends. A comparison might be made between masses of tracheids and masses of organ pipes. We are now looking down into the pipes from above. The primary function of the tracheids is the conduction of water, though they also serve for mechanical support. We shall soon see that the lateral walls are covered with curious markings, called *bordered pits*. Many times these can be detected in cross-section, but they will be better understood when studied in face view.

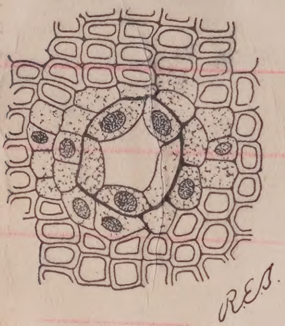

FIG. 108. — Cross-Section of a Vertical Resin Canal of Pine Wood. Parenchymatous secretory cells surround a central cavity into which they pour resin (pitch).

Traversing the mass of tracheids are the wood rays which have been observed already in the phloëm. They consist of chains of living cells, and every tracheid somewhere in its length touches a ray cell. Some of the wood rays run from cortex to pith, but others run for varying distances inward. The cambium always forms the rays, and as the stem increases in circumference it initiates new ones whenever needful.

If the twig is more than one year old, the fact will be evidenced by what are called *annual rings of growth*. The cambium of all our northern trees is of course subjected to a periodical inhibition of its activities. With the coming of spring its starts growth vigorously and lays down a band of large, thin-walled tracheids around the trunk and around every root and twig. These constitute the *spring wood*. As the summer advances, the tracheids decrease in size, their walls become much more thickened, and they are usually more elongated in a direction at right angles to the rays than in their radial diameter. Cambial activity ceases by midsummer while the plant prepares itself for another year. The transition from the small, thick-walled summer tracheids of one year to the large, thin-walled tracheids of the next spring is necessarily very abrupt and the result is that the yearly increments in growth are easily seen even with the naked eye. Due to the difference in density of the two regions they absorb stains or varnishes quite differently and this leads to the beautiful wave patterns seen on boards of polished wood (longitudinal sections).

One more conspicuous structure appears in pine wood and that is the resin canal (Fig. 108). All that was said of the cortical resin canals applies to this also. Not only does the resin canal run vertically through the tree, but there is also a horizontal or radial system of like nature which links up with the vertical one. Let the student imagine a series of gas-pipes set up in concentric circles; then let the members of one circle connect horizontally at intervals with the members of another circle, at various heights both inside and outside, and a fairly accurate model of the resin canal system will be visualized.

Approaching now the inner regions of the twig, we note that the tracheids are decreasing in size and as we come to the border of the pith they become very small (Fig. 104). These smaller, inner tracheids constitute the *primary xylem* and have quite a different origin from the great mass of the outer tracheids (*secondary xylem*). They were, in fact, derived from the primary or apical meristem and not from the cambium. They are of trifling physiological importance, yet they possess great evolutionary significance.

The *pith* which lies on the very inside of the twig resembles the cortex in its histological features. Its cells are parenchymatous, circular to oval, and protoplasmic. The pith is utilized chiefly as a storage tissue.

C. THE DETAILED STRUCTURE OF PINE WOOD

From the preceding study we derive only a very imperfect idea of wood structure. For let it be clearly realized that we have seen but a cross-section of the elements — just the sort of view one would get by looking at the cut surface of a tree stump. To find out what is the actual structure of the wood we must study it in two other planes of space and then mentally reconstruct the idea of a solid body. The student need not feel alarmed if he encounters difficulties in this attempt at first — such is the universal condition. Persistence will, however, overcome the difficulty and the gain arising from this ability to visualize three-dimensionally is incalculable. It should be realized that we never really *see* the three dimensions of any physical body. It is all a question of reconstruction in the "mind's eye." The concept of solid bodies is not arrived at through sight alone, but is built up mostly from the synthesis of tactual and visual percepts.

The tree stem is a cylinder, and three sections passed through it will reveal all the features of its anatomy. We have already studied the cross or transverse section and realize that we have looked down upon the cut ends of thousands of cells, many of which are much more elongated in the vertical than they are in the horizontal plane.

Longitudinal sections of the stem are cut at right angles to the transverse section and are of two kinds. Any longisection which passes from the center of the stem outward to the periphery is logically called a *radial section,* since it follows a radial plane. Any longisection which does not pass through the center, but instead cuts along a line parallel to a diameter is called a *tangential section.* The latter is the type of cutting which the lumberman calls plain sawing; the first section of this sort which would be cut from a log he would call a "slab."

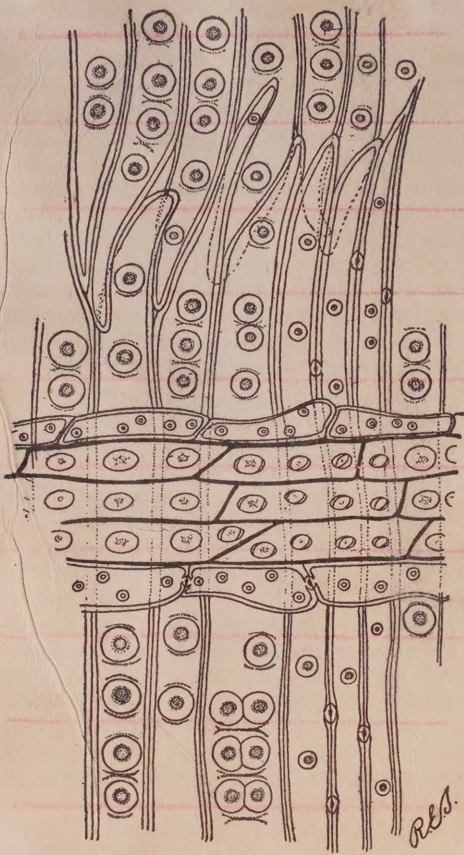

FIG. 109. — Radial Section of the Wood of White Pine (*Pinus Strobus*). The vertical elongate cells with tapering ends are tracheids. They bear bordered pits associated with "bars of Sanio." Horizontally runs a wood ray. Its parenchymatous cells bear large pits, and it is accompanied by a single row of marginal tracheids above and below.

Let us replace the cross-section beneath our microscope with a radial one. At first glance it is hard to realize that the section is related to the one just studied (Fig. 109). For now the tracheids appear elongated like pipes; in pine wood they are about four millimeters long. They taper to blunt and rather curved extremities, and their faces are beset with curious eye-like markings — the *bordered pits* — oddly complex structures through which water is conducted from one tracheid to another. Each consists of a hollow, low dome something like a blister which protrudes into the tracheid; it is formed as a part of the secondary thickening layer of the cell wall. In the top of the dome is a small opening, and across its floor, so to speak, is stretched the middle lamella, here called the *pit membrane*. It usually bears in its middle a thickened area called the *torus*. The bordered pit of one tracheid is exactly matched by another bordered pit which bulges into the adjoining tracheid. The following imaginative excursion from one tracheid to another through a pit will, perhaps, make their structure more intelligible. Suppose we found ourselves inside a giant tracheid; all along the radial walls on either side would be seen rows of low domes, each with a hole in the top. Approaching one of the domes and passing through its opening, we find ourselves in a chamber which is slightly arched behind us where we entered. Straight in front stands a circular diaphragm or plate in the center of which is a slightly raised or bossed area. The diaphragm is the pit membrane (really the middle lamella), and the elevation is the torus. Radiating from the torus we also observe many small and slit-like pores in the membrane. Passing through one of these, we enter the bordered pit of the adjoining tracheid; ahead arches up the dome with the hole in its roof; behind us lies the pit membrane with its torus.

Other conspicuous features of the radial section are the wood rays which appear as ribbon-like bands lying at right angles to the course of the tracheids. They stretch for a considerable distance and often cross hundreds of tracheids, though very naturally it is difficult for a plane section cut with a knife to follow them in their full course. It is the large, radially arranged rays that make certain woods so easy to split. The wood ray of the pine as seen in radial aspect is made up of rectangular parenchymatous cells which possess cytoplasm and nuclei. The pits on their faces are conspicuously large and are called *oöpores*. The ray varies in its vertical height from one to several cells. Along its upper and under border run one or two rows of short cells, quite different from the other elements of the ray. They are called *marginal tracheids* and are wholly limited to certain coniferous woods. It can be determined that like the vertical tracheids they bear bordered pits, that they are without protoplasm, and that their walls are lignified. As to the phylogenetic origin of marginal tracheids there is not much question. They seem to have been derived from tips of the ordinary tracheids which bent over to follow the ray in its course and were subsequently cut off and slightly modified. Their function, like that of their parents, is water conduction; they form a quick and effective method for transferring water radially through the wood.

Finally, we may note the resin canal in its longitudinal aspect. It is essentially a channel surrounded by secretory cells.

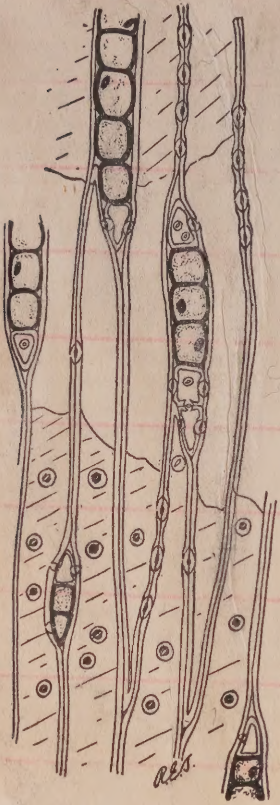

FIG. 110. — Tangential Section of White Pine Wood. The tracheids below belong to the summer wood, and in this species of pine they bear scattered and small bordered pits on the tangential walls. The spring tracheids are pitted only on their radial walls. Rays with accompanying marginal tracheids are evident. The most central ray has a double row of marginal tracheids below — a not uncommon condition.

The tangential section is the last to be considered (Fig. 110). Most of the tracheids now show no pits in surface view; they are seen in section, however, on the radial walls. Into the lumen of each tracheid rise two slight spurs (sections of the dome of juxtaposed pits), while between them lies the sectioned pit membrane with its spindle-shaped torus. If the pit membrane lies in the center between the bordered pits, the section was cut from sap-wood; if on the contrary, it bulges out and is blocking up one of the pit mouths, the section is from a piece of heart-wood.

The ray in the tangential aspect has an entirely different appearance from that of the radial section. It now consists of few to several cells in vertical sequence one above another. The upper and lower ones are smaller and hence the mass appears slightly spindle-shaped. Careful study will show that the uppermost and lowermost cells are lignified — they are of course the marginal tracheids.

We have now studied the ray in its three aspects and have all the data necessary to visualize it properly as a three-dimensional body. Yet the writer knows through long experience that most students have great difficulty in grasping this concept. A few comparisons may help. The pine ray has the shape of a thin knife blade stuck into the tree radially, or it is like a low wall, one brick in thickness and several bricks high, which runs radially into the tree. In transverse section we look at the top of the wall; in radial section we see its side; in tangential section its end.

74. *The Wood of the Oak — An Angiospermous or Hard Wood*

For comparison with the relatively simple wood of the pine we may now study the more complex structure of oak wood.

If we examine with the naked eye or with a simple lens a block of oak so prepared as to show the three important aspects, it is surprising what an amount of gross detail becomes visible. The annual rings are delimited by the relatively large pores which characterize the spring wood. These are the openings of the *vessels* or *tracheæ*, elements which do not occur in the pine. In addition, the surface of the block can be seen to exhibit a delicate mottled effect. Around the vessels and running as minute tongues into the summer wood are areas of paler tissue. These are made up of tracheids similar to those of the pine. The darker patches, however, which are interspersed among them, are composed of *fibers* which belong to the category of mechanical tissues. Rays, too, are evident and are of two sorts — minute ones like those of pine, called *simple* or *uniseriate rays* and, in addition, much bolder ones which form conspicuous stripes across the block. The latter constitute *compound* or *multiseriate rays*.

On the radial surface of the block the vessels can be traced downward as tiny grooves and slits. The simple rays are also visible as a delicate striping, while the compound rays form broad conspicuous bands or flakes across the block. This is the aspect of oak wood which is known in the trade as quarter-sawed oak. Quarter-sawed or quartered oak is so called because in sawing it the log is first split lengthwise into four quarters, then boards are cut from the flat faces of the resultant wedges of the cylinder. This produces the closest approximation to a radial section that it is possible to saw out and when the boards are stained and polished the compound rays are revealed as striking, glossy flakes and bands.

In the tangential section, the compound rays are visible as large spindle-shaped bodies. The familiar mountain and valley effect seen on tangential sections of wood (plain sawed boards) is due to the difference in density of spring and summer wood. The shape of the trunk of a tree is that of a much-drawn-out cone. The terminus of the shaft is but one year old and has but one annual ring of wood; the base, on the other hand, may have a hundred annual rings, depending, of course, upon the age of the tree. Hence the annual layers of wood all incline gently inward and a board sawed out in the lumber yard necessarily bears the wave effect to which we referred. Of course any bend or twist in the "grain" will introduce curious modifications into the markings.

The student should practice interpreting the markings on doors, window casings, and table tops till he can account for each type. He will find that in nearly every case where valuable woods are used they are cut into thin sheets known as veneer and glued over a cheaper wood. Solid mahogany, rosewood, or ebony is rarely found.

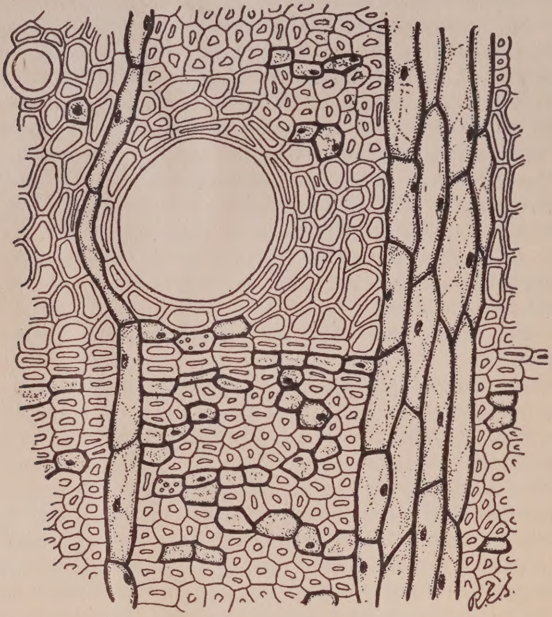

FIG. 111. — Cross-section of Wood of Red Oak (*Quercus rubra*). Summer wood below, spring wood above. Wood fibers with thick walls and interspersed with wood parenchyma; a large spring vessel surrounded by tracheids; simple and compound rays, are represented.

Let us now turn to the compound microscope. As the cross-section flashes into view, we are at once impressed by what we had been led to expect from the naked-eye observations, viz., that oak wood is decidedly more complex than pine (Fig. 111). The great vessels are most conspicuous, and it will be seen that they occur not alone in the spring wood, but that they also run into the summer wood, though in the latter they dwindle in size and have much thicker walls. A small summer vessel is shown in the upper left-hand corner of our figure.

Around the vessels are areas of tracheids similar to those of the pine, though less regularly arranged. In the summer wood, particularly, they are interspersed with masses of densely packed and smaller, thick-walled wood fibers. Scattered through the whole section and particularly noticeable among the wood fibers are cells with far thinner walls which contain protoplasmic contents. These constitute *wood paernchyma.* The two sorts of rays — simple and compound — are conspicuous. The reason for the other terms, uniseriate and multiseriate, applied to them now becomes evident.

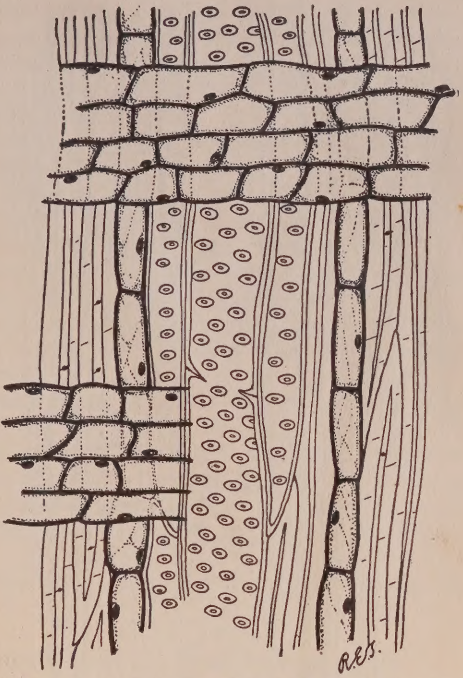

FIG. 112. — Radial Section of Wood of Red Oak. From left to right the longitudinal elements in the middle of the field are respectively: wood fibers, wood parenchyma, tracheid vessel, tracheid fiber, wood parenchyma fibers. Portions of two simple rays run horizontally.

As we turn to the radial section, all the above elements are seen in their longitudinal aspect (Fig. 112). The vessels pass like great slits through the section, since they are often so large that they are cut through their middle without including either the front or back. This view permits the study of several of their significant features. First it may be noted that they are constricted at intervals and that rather prominent spurs run into their lumina from the constrictions. In case the front or rear wall is present, the spurs show themselves to be sections of annuli. The whole vessel might be compared to a set of barrels standing one on another and having the bottoms and tops knocked out. In fact the comparison is even closer, for the spurs actually do mark the remains of cross walls which have been dissolved away so that what were originally, in the meristematic state, chains of short cells, are now merged into a continuous channel. Vessels are some ten centimeters long on an average, though cases are known where they attain a length of a meter or even two meters. Their walls bear many tiny and crowded bordered pits: this declares their affinity to the tracheids from which they were phylogenetically derived. They serve for water conduits and confer upon angiospermous woods a far greater efficiency in water conduction than is possessed by the wood of conifers.

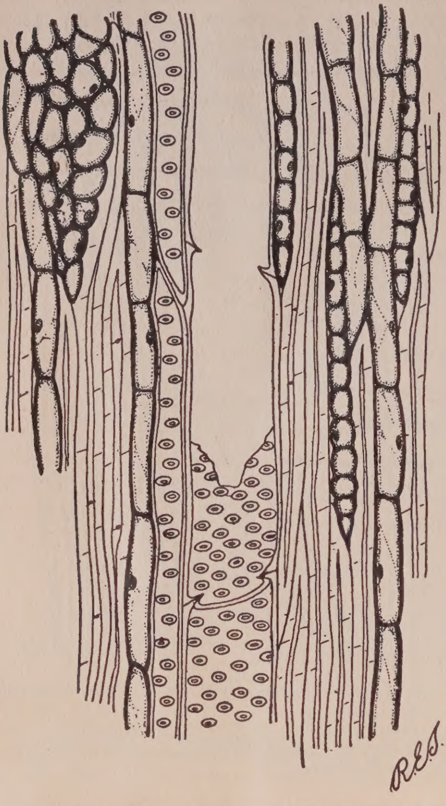

Fig. 113. — Tangential Section of Wood of Red Oak. Chains of wood parenchyma, three simple rays, and a portion of a compound ray are seen associated with fibers, tracheids, and a vessel.

The tracheids, though smaller than the vessels, bear the same border-pitted markings and also assist in water conduction. The fibers, as we have suggested, are elements introduced to subserve the mechanical function of support. Perhaps we may see a relation between the introduction of vessels and the addition of fibers, for it is obvious that the former tend to weaken the stem, while the latter restore the lost rigidity. The distribution of fibers along the outer part of each annual ring is another feature which follows the best architectural principles, since a cylinder stiffened on the outside, or —

what is essentially the same thing — a hollow cylinder, is stronger than a homogeneous or a solid one. We shall later find the same principle applied to the construction of herbaceous and slender-stemmed plants. Fibers in longisection are seen to be slender, much elongated elements, which are densely felted together. They may bear a few abortive bordered pits on their walls, for the oak scarcely has true wood fibers. It possesses instead what are called *fiber tracheids*. These represent an evolutionary advance from a tracheid in the direction of a not yet fully perfected fiber.

The wood parenchyma now appears in the form of vertical chains of slightly elongated protoplasmic and nucleated cells. They belong to the category of storage parenchyma and, in the winter particularly, will be found full of starch. The chains of wood parenchyma link up in some part of their course with the rays.

The rays themselves do not differ essentially from those of the pine, except for the fact that they have no marginal tracheids. They are bands of simple pitted conducting and storage parenchyma. The compound rays appear in radial aspect as wider bands of cells crossing the longitudinal elements.

A detailed description of the tangential aspect is not necessary, for all the elements except the rays are essentially cylindrical and will not differ in the tangential view (Fig. 113). As for the rays themselves, the simple ones are similar to those of the pine, while the compound ones are grouped in systems and run for considerable vertical distances. They show thousands of cells even in tangential aspect.

Fig. 114 is a stereogram of a small block of oak wood showing the three important faces.

75. *The Historical Origin of Angiospermous Woods*

It has just been pointed out that the wood of the oak — a typical angiospermous wood — is distinguished from that of the pine by a greater histological complexity. Most conspicuous, perhaps, and always serving to distinguish angiospermous woods from gymnospermous, is the vessel. Fibers are also confined to angiosperms, though wood parenchyma is not.

A. THE VESSEL

The phylogenetic origin of all the above histological elements has been determined by botanists, and the story is one of great interest. The vessel, as we have already said, comes into existence through the removal of end walls of tracheids, which lie in chains. All stages of this process can be traced in the ontogeny of certain woods (Fig. 115). Originally the tracheids are linked end to end by bordered pits; in their transitional stages to vessels, the borders of the pits and the pit membranes disappear. Then the wall substance separating the pits dissolves, and the result is either a large circular opening or, since the pits often lie in transverse rows, a fused series of elongate, slit-like pores on the separating walls. The former type of opening is called a *porous perforation* (Fig. 115, D); the latter constitutes the *scalariform perforation* (Fig. 115, F). The scalariform perforation may subsequently break down its rungs to form the porous type.

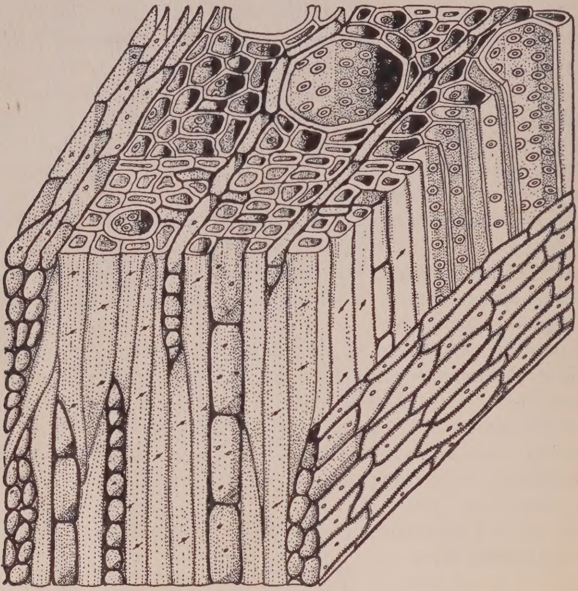

FIG. 114. — Stereogram of a Small Block of Oak Wood.

B. THE WOOD FIBER

Wood fibers are also derived from tracheids. In the oak they are really in a transitional state and constitute fiber tracheids. The evolution of the wood fiber only involved elongation, thickening of the wall, and the reduction of bordered pits to simple pits.

C. THE WOOD PARENCHYMA

The story of the evolution of the wood parenchyma is perhaps the most interesting of all. In the root-wood of the spruce (*Picea*), it is found that in the last row of tracheids laid down by the cambium each year there are interspersed certain elements which while still meristematic become transversely septate, and so divided up into rows of short segments. In some of the cells so resulting the protoplasm persists, and the result is a true wood-parenchyma cell; but in other segments the protoplasm lays down a heavy lignified wall which it sculptures with bordered pits (Fig. 116, C). Hence, these segments become short tracheids with horizontal end walls. At maturity, then, we find interspersed among the terminal tracheids of the annual ring these transversely septated elements which have the shape of a tracheid but whose segments may be either parenchymatous or tracheidal. This condition in *Picea* would not seem to be the most primitive one, for there must have been an antecedent state when none of the

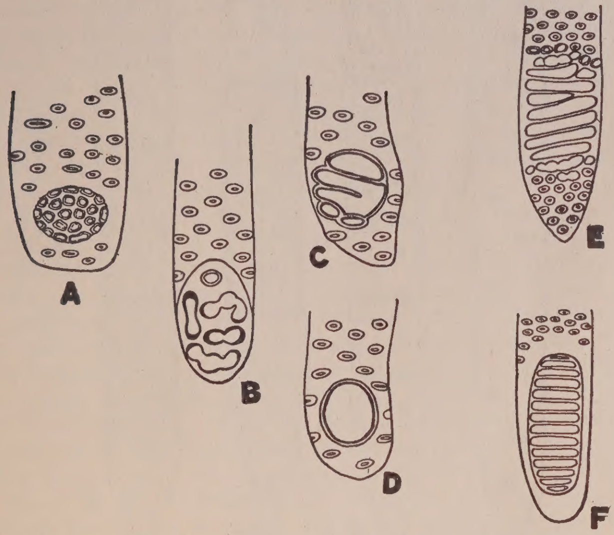

FIG. 115.—The Origin of Vessel Perforations in Angiosperms: A, incipient perforation in young wood of *Pelargonium;* B, more advanced stage of perforation from young wood of *Potentilla monspieliensis;* C, later stage from wood of *Pelargonium;* D, completed perforation from older wood of *Pelargonium;* E, scalariform perforation from *Alnus japonica* in advanced stage of formation; F, completed scalariform perforation in wood of *Alnus japonica.*

segments of the septated tracheid had become parenchymatous. In 1917 a wood possessing this feature was found in the Lower Cretaceous deposits of Texas.* Its terminal tracheids were septated, but all were still of tracheidal nature (Fig. 116, B). The genus of plants which bore this wood has been called *Telephragmoxylon* ("end" + "split" + "wood"). It is evident that *Telephragmoxylon* represents a more primitive state of tracheid septation than does the spruce.

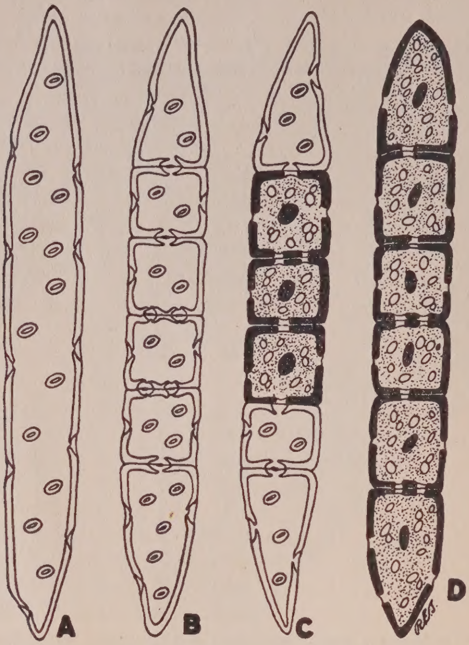

FIG. 116. — The Evolution of Wood Parenchyma: A, tracheid of a coniferous wood — the element from which wood parenchyma arose; B, septated tracheid of *Telephragmoxylon brachyphylloides*, a fossil wood which was found in Texas in deposits of the Cretaceous Period; C, septated and partially parenchymatized tracheid of spruce wood (the cellulose-walled segments contain stored starch grains); D, fully parenchymatized tracheid (a chain of wood parenchyma) from the hemlock. (Redrawn from Jeffrey.)

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* R. E. Torrey, "*Telephragmoxylon* and the Origin of Wood Parenchyma," *Annals of Botany*, XXXV, 73–77, 1921.

E. C. Jeffrey, "The Origin of Parenchyma in Geological Time," *Proc. Nat. Acad. Sci.*, XI, 106–110, 1925.

We can also trace the evolution of wood parenchyma forward from the spruce condition. In certain close relatives of the spruce, such as the larch, the terminal parenchyma rows still conform to the shape of a tracheid, but there are never any short tracheids among them; the septated tracheid has become wholly parenchymatized (Fig. 116, D). The next step taken in evolution can be seen in many conifers which belong to the group of which junipers and arborvitæs are representatives. It is also the condition possessed by the oak. Here the wood parenchyma has departed from its strictly terminal position and is distributed through the whole body of the annual ring. Parenchyma in such a state is said to be *diffuse*. One last step completes the story: in certain of the higher angiosperms the parenchyma comes to form sheaths around the vessels. It is then said to be *vasicentric*.

The progressive evolution and distribution of wood parenchyma can be nicely correlated with the progressive cold which crept over the earth with the oncoming of the Glacial Period.

The ancient Paleozoic trees had no wood parenchyma. Their woods were essentially in the condition of the pines, made wholly of tracheids and wood rays. In the Mesozoic the first breath of the cold began to creep over the earth. This must have introduced a short resting season during which the trees shed their leaves and waited for the spring. With the return of the growing season, it would be to the obvious advantage of a plant to relay its ascending nutritive sap as rapidly as possible to the developing cambium. This could be facilitated by slowing up the sap current in the terminal tracheids of a ring, since these abut directly on the cambium, for the sap would thus be given a chance to osmose more readily into the living cells. Thus arose *Telephragmoxylon* with its septate tracheids. For rapid growth food is also necessary, and it may easily be realized that a supply of food as well as water in cells bordering the cambium will be of distinct value to the plant. Foods can be stored only in protoplasmic cells, hence the conversion of certain parts of the septated tracheids into wood parenchyma. The progressive parenchymatization of the tracheid would be more and more advantageous, and the final multiplication and diffusion through the xylem would permit of the storage of far greater quantities of food. This could be relayed in spring through the rays to the growing cambium and to the developing apical meristems. It will be clear, then, that the whole evolution of the longitudinal storage elements of wood can be related to the progressive refrigeration of the pre-Glacial climate. We shall soon realize that a striking and final modification of the storage parenchyma system brought our modern herbaceous vegetation into existence.

D. THE WOOD RAY AND ITS EVOLUTION

One more characteristic feature of wood demands discussion, and that is the ray. Here again striking evolutionary principles can be traced. The uniseriate or simple type of ray is a very ancient structure. In the most primitive known trees, which lived even before the Coal Period, we catch a glimpse of the probable origin of the wood ray. Like vessel, fiber, and wood parenchyma, it had its genesis in the tracheid. We are aware that tracheids have a distinctive sculpturing on their walls. This may consist of bordered pits, though in more primitive regions of the wood and in ancient forms the sculpturing was largely spiral or scalariform. In the root-stock of one group of ancient plants known as *Lepidodendra* the rays also bore spiral markings, and the inference is that they, too, arose from tracheids which turned aside from the vertical into the horizontal position and were utilized for water conduction in a radial direction. We have seen already that the marginal tracheids of the pine arise in exactly the same manner.

The original ray was simple or uniseriate, but like the wood parenchyma was profoundly affected by the oncoming of the cold.

(1) *Leaf-trace and Leaf-gap.*

Before we discuss the modifications of the rays, however, it will be necessary to consider the leaf-trace in plants and its relation to the wood, for the modifications of rays are intimately related to leaf-traces. Fig. 117 is introduced to make the following discussion more intelligible. The *leaf-trace* is the strand of wood and phloëm which detaches itself from the stele and rises obliquely through the cortex to enter the leaf. Since the leaf is formed on the very youngest twig, the leaf-traces must necessarily be about the first vascular structures which differentiate from the apical meristem and appear in a young stem. Consequently in any internodal cross-section they will be seen as a circle of small wood-and-phloëm areas bordering the pith. Those which are to pass off into the leaf at the next node will be larger and more striking; those which are to pass into leaves farther up will be less strongly developed. The leaf-traces are bound into a complex system which expresses the phyllotaxy. If, then, it were possible to dissect out the vascular system of a young twig entire as a free preparation, one would see a complex network of leaf-traces based on a definite pattern. As has been said, leaf-traces are formed from primary meristem. Very soon the cambium becomes active around the whole stem and begins to lay down secondary wood outside the primary wood of the leaf-trace. Secondary phloëm is likewise added to the inside of the primary phloëm, which is consequently shoved progressively outward and is usually crushed and destroyed in the process.

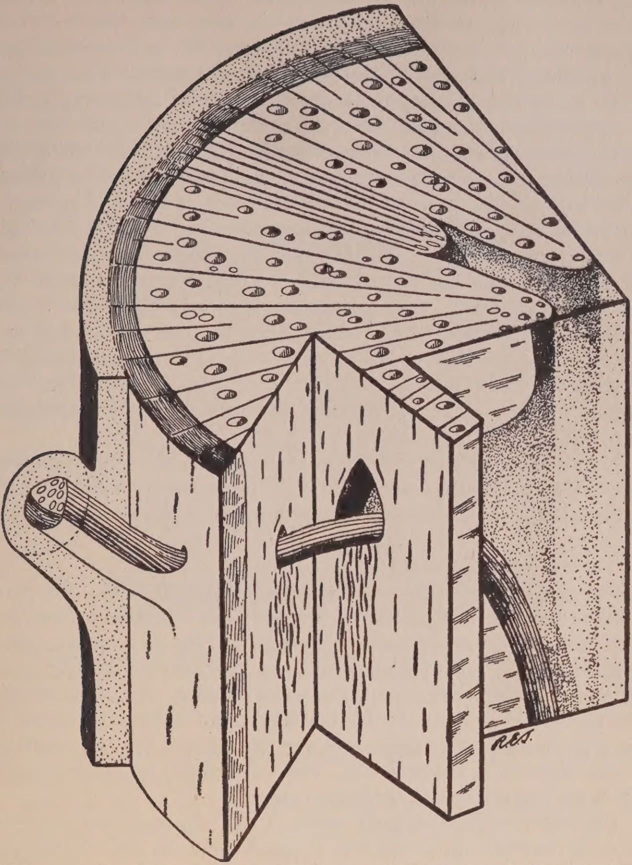

FIG. 117. — Stereodiagram of a Portion of a One-year-old Twig to Illustrate the Course of a Leaf-Trace and Its Relation to Leaf-Gap and Leaf-Ray. The block is represented with a thin plate of wood extended into the foreground. The leaf-trace of primary wood rises at a gentle curve from beneath, turns abruptly outward and, accompanied by the diminishing leaf-gap, runs through the secondary wood. As it leaves the stele to enter the leaf petiole, a strand of phloëm tissue is added to its underside. On the tangential surface of the vertical plate of wood the aggregate storage ray is evident, while on the upper surface of the block the cross-sectioned aspect of a leaf-trace cut considerably below a node is represented with its accompanying aggregate ray.

The result is that the primary wood of the leaf-traces becomes sealed inside an ever-thickening band of secondary wood. As the stem increases in girth through the summer, the leaf-traces elongate to keep ahead of it and to maintain their connection with the leaf. With the coming of autumn, however, the leaves fall away, and the traces elongate no more and are of no further value.

The term *leaf-gap* now needs definition. As the wood of the leaf-trace starts from the outer margin of the pith to take its outward course through the secondary wood, its place of exit and passage is marked by a gap which appears in the xylem and which is filled by a projecting tongue of pith. The gap runs but a short distance outward, and after the trace has accomplished its exit, the gap is sealed over with secondary wood. In any cross-section made just below a node, the leaf-gap will appear as a radially extended arm of pith just as it does on the upper surface of Fig. 117. It is subtended outwardly by the sectioned leaf-trace. In tangential section it appears as the lance-shaped "window" shown in the thin plate of wood which extends into the foreground of the diagram.

The woody segment laid down by the cambium outside the leaf-trace often differs markedly from the rest of the secondary wood, and this modification tends to persist for many years after the leaf has fallen.

(2) *The Aggregate Ray.*

The conifers, as we have seen, possess simple rays. In many primitive angiosperms, however, we find that the rays in the leaf-trace segment just mentioned have begun to take on a curious effect. They are still individually uniseriate, but they become densely aggregated, so that the leaf-trace segment exhibits a striate appearance even to the naked eye. Under the compound microscope it can be seen that in their aggregate state the individual rays are separated by only one or two tracheid files. Fig. 117 exhibits the aggregate ray in both its transverse and tangential aspects.

The superior physiological value of the *aggregate ray* over the simple is evident. Since the leaf is connected with the manufacture of food, the best and nearest storehouse for food would naturally be the pith inside, and also the woody segment outside the leaf-trace. As we are aware, the rays are always utilized for the storage function, and consequently their multiplication will constitute a superior food-storage mechanism just where food is coming in from the leaf.

The *compound ray* follows very naturally from the aggregate condition and represents the state in which the tracheids included among the ray aggregation just described have also been converted into parenchymatous tissue, the result being the broad sheet of parenchyma denominated the compound ray. This is, of course, a better storage device than that of the aggregate condition.

In the ontogeny of an oak stem all transitions from the aggregate to the compound ray are easily seen. The aggregate ray persists for about three years and then gradually compounds; it is easily recalled by wounding (traumatic reversion). It is known, too, that in the Miocene Period oaks had aggregate rays as do also the southern oaks of the present day. Clearly we have all the links of a chain of reasoning which tends to prove that the compound ray is an evolutional derivative of the aggregate.

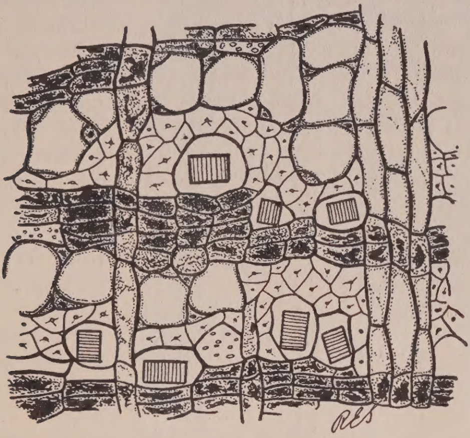

FIG. 118. — Phloëm of the Linden (*Tilia*) in Cross-section. Portions of two annual rings are represented. The dark horizontal bands are of phloëm parenchyma. Crystallogenous cells and phloëm fibers are evident; the largest elements are sieve cells accompanied by small companion cells. Portions of three rays are also seen.

There is one other kind of ray system associated with leaf-traces. It is called the *diffuse ray* and is characteristic of many of our forest trees.

76. *The Phloëm of Angiosperms*

The phloëm or bast of angiosperms, like the wood, is histologically more complex than that of gymnosperms, since in addition to sieve cells and phloëm parenchyma it possesses so-called companion cells and bast fibers.

The phloëm of the linden tree (*Tilia*) is particularly good for an introductory study, since its elements are large and striking and stain very sharply (Figs. 118, 119). In young linden twigs the phloëm is divided into wedges by the flaring wood rays (Fig. 120), but in old stems it becomes a continuous layer. Under the microscope a transverse section shows a banded structure, since the various tissues are laid down in successive layers. The sieve cells are conspicuous because of their large size. They differ slightly from those of the pine in that their functional sieve plates are larger and confined to their oblique end walls. In their angles one often detects small *companion cells* which in sectional aspect look as if they had been cut out of the corners of the sieve cells. This appearance is based on a truth — they really have arisen through a mitosis which cuts them off from the young sieve cells, which curiously enough lose their own nuclei subsequently and contain only cytoplasm. Hence, the nuclei of the companion cells must preside not only over their own functions, but over the activities of the cytoplasm of the sieve cells also.

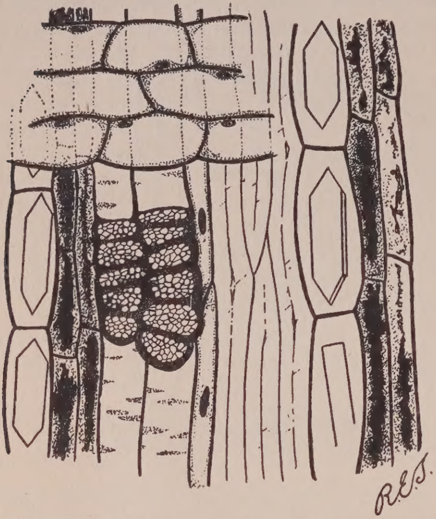

Fig. 119. — Radial Section of Linden Phloëm. From left to right the elements represented are: crystal-cells, phloëm parenchyma cells, two rows of sieve cells with their sieve plates heavily outlined, nucleated companion cells, bast fibers, crystal cells, and phloëm parenchyma. A fragment of a ray lies in the upper left-hand part of the figure.

The phloëm parenchyma of *Tilia* is differentiated into two kinds: one is similar to that found in pine, while the other is composed of larger cells which contain wonderfully perfect elongate and pointed crystals of calcium oxalate. A row of this *crystallogenous phloëm parenchyma* is laid down at the end of each season's growth. Also, the *Tilia* phloëm contains masses of *bast fibers*. These are long, slender cells belonging to the category of supporting tissues and are densely packed together in masses. They consist of little but lignified wall substance. Their tensile strength is remarkable, being far superior to steel threads of an equal size. The bast fibers of many plants furnish valuable textile materials. Linen is made from the strands of bast derived from the flax (*Linum usitatissimum*). Their constituent cells are from twenty-five to thirty millimeters long and have a diameter of about .0241 millimeter.

77. *The Herbaceous Stem and Its Origin*

Up to this point we have concerned ourselves wholly with woody stems, that is, with stems which live year after year and which lay down successive annual rings of wood. Such a stem, based on the *Tilia* tree and in highly conventionalized stereogram, is shown in Fig. 120. The black central cylinder represents the woody core, the vessels of which are shown as white dots. For the sake of simplicity the wood rays are omitted. On the left, three leaf-traces destined to enter a leaf are passing from the cylinder. Each is subtended inside by an arm of pith (leaf-gap). Such traces rise in a gentle curve and finally detach themselves from the cylinder to enter a leaf petiole. A strand of phloëm accompanies them in the outward journey through the cortex. After their exit the leaf-gap closes.

A more prevalent type of vegetation in our temperate climates, however, is the herb whose slender, soft, and usually vigorously branching stem lives but one season, though the underground parts may be perennial. The term *herb* is not susceptible of sharp definition, since transitional types of stems link up with the woody tree.

Herbaceous plants are distinctly modern and do not seem to have been an element of the earth's earliest angiosperm flora. Their evolution is associated with the advent of a winter season, and though they came into existence in high latitudes, they have now forced their way southward and have entered the tropics. It would seem to be only a question of time till they finally assert their supremacy over the woody forms and become the dominant angiospermous type.

The study of the leaf-trace of trees and the associated compound storage ray has placed in our hands the key to the structure of herbaceous stems. They but continue the story started among woody forms and bring it to its logical conclusion.*

The factors which have been at work to mold woody plants into herbs are essentially the following:

(1) Increase in storage parenchyma, leading to a progressive reduction of tracheidal tissue.

(2) Gradual restriction of secondary growth till finally cambial activity is completely abolished and only primary tissues remain.

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* E. C. Jeffrey and R. E. Torrey, "Transitional Herbaceous Dicotyledons," *Annals of Botany*, XXXV, 227–249, 1921.

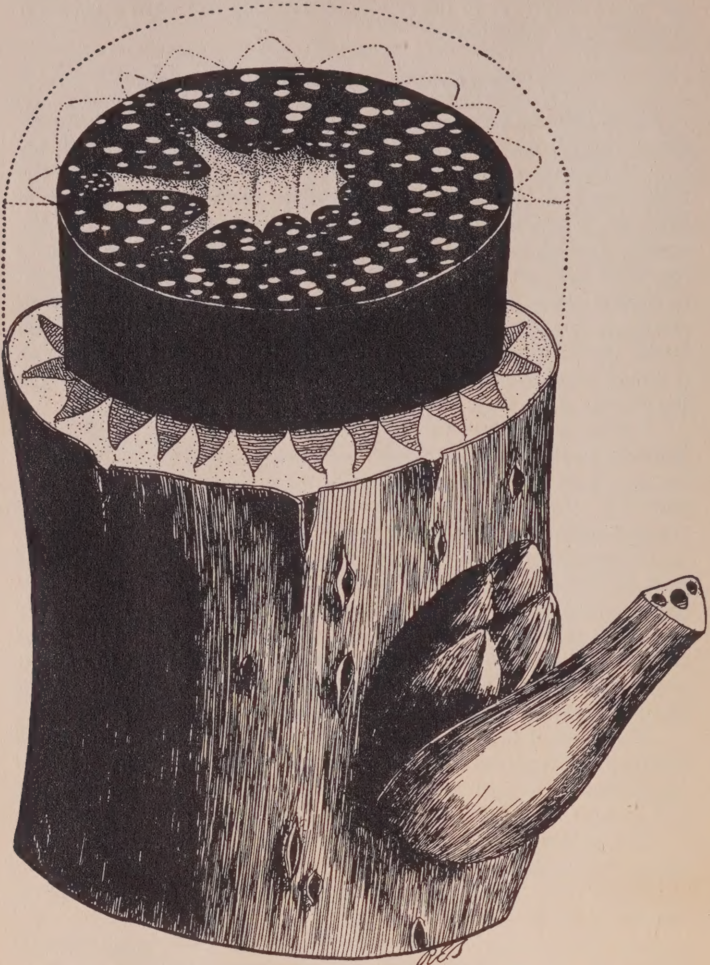

FIG. 120. — Stereodiagram of a One-Year-Old Twig of the Linden. Explanation in the text.

A. A TRANSITIONAL HERB

The story of the origin of the herbaceous stem is difficult to put into clear-cut words, since it involves a description of a rather complex three-dimensional body. To assist the imagination Fig. 121, a highly conventionalized stereodiagram of a semi-herbaceous stem, such as that of the aster, is introduced. Careful study of this figure in comparison with Fig. 120 of the more primitive tree ought to make

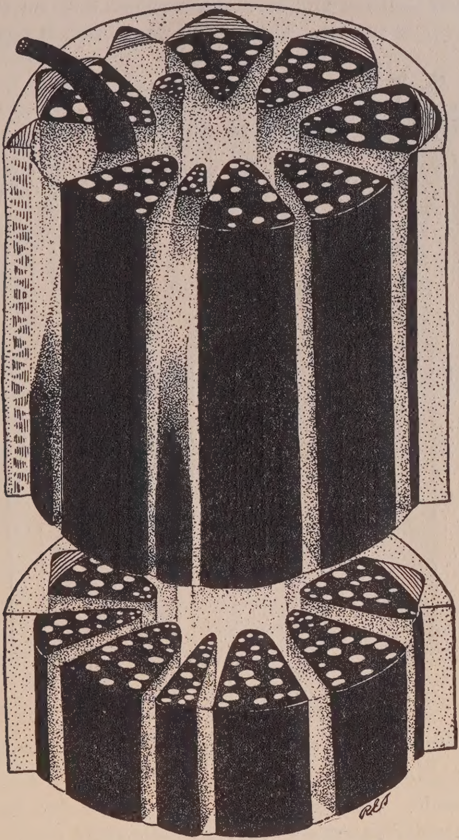

Fig. 121. — Stereodiagram of a Semi-Herbaceous Stem Based on the Aster. Explanation in the Text.

its basic structure plain to the student and at the same time help him to understand the really astonishing correlation between paleoclimatology, stelar morphology, and physiology. The wood, as before, is represented in black; storage parenchyma is stippled. The extraxylary tissues (phloëm and cortex) are shown only on the posterior part of the upper surface. The upper cross-section is supposed to be taken at a node. The right half is occupied by five *fibro-vascular bundles* represented as wedges with conventionalized vessels and separated by radial bands of parenchyma. On the left, however, three leaf-traces are entering from a leaf. The woody strand of the middle one is shown extended as if coming from a petiole; the laterals are represented in section. The significant thing about these three traces is their small size, for not only are they flanked with parenchyma, just as are the larger wedges, but they are also bounded with parenchyma

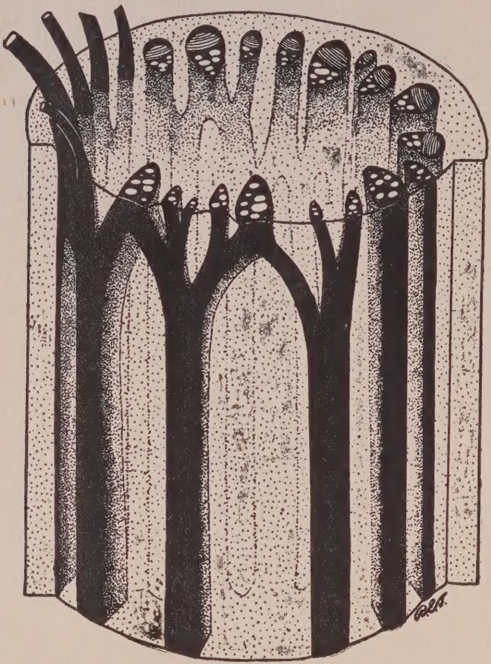

FIG. 122. — Stereodiagram of an Extreme Herbaceous Stem Based on the Buttercup. Explanation in the text.

outside. If we follow them downward through the transparent "sea of parenchyma," it will be observed that their radial diameter increases till in the lower cross-section they have become just as deep as the other wedges, though they are still a bit narrower. In other words, the outer parenchyma has been replaced by wood. Right here is the crucial point in the evolution of the herbaceous stem. The leaf-trace running in from the large and efficient leaves is carrying abundant sugar. This is not all needed for immediate growth, and consequently much of it must be stored in the form of starch. Now it is obvious that the easiest place to store it will be right in or around the leaf-trace itself. But dead vessels and tracheids cannot store starch. What, then, is to be the solution of the problem? Why, simply convert the outer part of the trace (fibro-vascular bundle) itself and the wood on both flanks of it into storage parenchyma — into a great compound ray. Our diagram shows that this was actually accomplished, and so the semi-herbaceous stem arose.

It should be noted that the flanking part of the storage tissue runs downward much farther than does the portion outside the trace itself, and that this is what divides the stele up into wedge-like compartments or the "fibro-vascular bundles" of the old morphology. The bands of storage tissue between the bundles were once called "primary medullary rays." Though their radial diameter may be increased by cambial activity, just as is that of the wood rays, they have nothing to do with the medulla and their phylogenetic origin is different from that of the true rays.

B. AN EXTREME HERB

The above discussion applies to what may be called a transitional herb. Let us now see what is to be found in ultimate herbs, taking the buttercup stem as an example.

Fig. 122, similar in conventions to Figs. 120 and 121, is a representation of the buttercup stem. At the left, five leaf-traces are coming in from a leaf and plunging into the sea of parenchyma. Since in the buttercup there is no boundary between pith and cortex, we are accustomed to speak of the whole mass as *fundamental* or *ground tissue.*

The significant thing about the fibro-vascular bundles is their reduced size. It was said above that one of the principles at work to turn woody plants into herbs was a progressive degeneracy of the secondary tissues, or what amounts to the same thing, progressive reduction of cambial activity. In the buttercup the cambium hardly functions at all, and consequently the fibro-vascular bundles are made up almost wholly of primary wood and phloëm (Fig. 123). This accounts for their small radial diameter. It should be noted, however, that in compensation for their reduction in size there has been an increase in number, so that the leaves of the plant may still receive plenty of food salts and water and have sufficient food channels through which elaborated foods may be sent back into the stem.

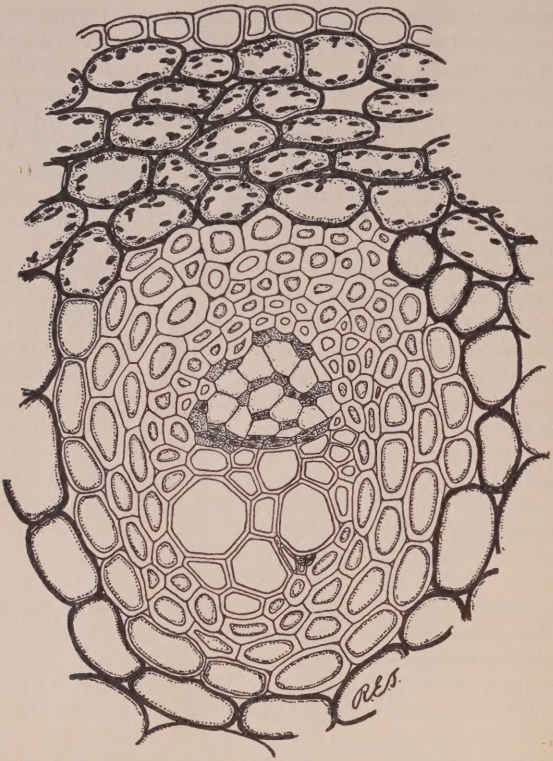

FIG. 123. — Cross-Section of a Single Fibro-Vascular Bundle or Leaf-Trace of the Buttercup Highly Magnified and with Its Accompanying Tissues. Epidermis and cortex are seen outside the bundle, while on both its flanks lies fundamental tissue (parenchyma). The bundle itself consists of a sheath of fibrous sclerenchyma surrounding the conducting tissues. The xylem is made up of vessels and fibers; the phloëm, of sieve cells and companion cells. The slight cambium has almost vanished.

The buttercup is an efficient herbaceous perennial plant. It produces quantities of seed and its stem is liberally provided with parenchymatous tissue for the temporary storage of starch during the early growing season. With the advance of summer this food is transferred to seeds, corms, or thickened roots. Our figure also shows that the fibro-vascular bundles are linked up with one another at the nodes.

In a sense such a reduction of tissues as has characterized the progressive evolution of the herb constitutes degeneracy and yet it would be far from the truth to speak of our extreme herbs as degenerate; it is better to use a term suggested by Professor Jeffrey and call them "dynamic herbs." They are extremely efficient plants, far superior to the more ancient tree. They have abolished all but the minimum of wood and phloëm necessary to carry on their activities of conduction; this permits them to build up their bodies rapidly just as soon as favorable conditions for growth arise. They are usually heavily beset with large and efficient leaves which form great quantities of starch. This is stored temporarily in cortex, pith, and leaf-rays and is transferred subsequently either to a host of seeds or to underground organs such as corms, bulbs, tubers, and rhizomes. The tree, on the contrary, devotes too much of its energies to the construction of a heavy mass of wood, most of which is all but useless after a few years. Its growth is slow and its adjustments to changing environments are not so rapid as those of the herb. It does not propagate itself so abundantly, and it seems destined to ultimate extinction.

C. THE STEM STRUCTURE OF MONOCOTYLEDONS

Thus far we have discussed the stem of the dicotyledons. We realize that they have finally become modified to a ring of separate fibro-vascular bundles or leaf-traces enclosing a pith and enclosed by a cortex. There is another type of stem in which a cross-section reveals many leaf-traces scattered through the whole area — in other words, they no longer stand in a circle, and the boundary between pith and cortex is not recognizable (Fig. 124). This type of stem structure is characteristic of the monocotyledons, though it is not strictly confined to them. It is considered by many textbooks to be morphologically distinct from the dicotyledonous type, but there is no real ground for this view. The scattering of the bundles of the monocotyledons is merely an expression of their multiplication. They become so numerous that they can no longer be accommodated in a ring and are consequently forced into the pith and cortex.

The leaves of monocotyledons are usually large and very efficient food-making organs. In order that this food may be conducted into the stem, many leaf-traces are necessary. The internodes are usually short, and as a consequence of these two factors — many traces and shortened internodes — the leaf-traces become very much crowded and are forced to leave the ancient circular alignment. Hence arises the stem with scattered bundles.

Another characteristic of the leaf-traces of monocotyledons is that they have no cambium and consequently they cannot grow after they are once differentiated (Fig. 125). As we have already seen, cambial activity is on the decline in extreme dicotyledonous herbs. The monocotyledons merely attain the logical (orthogenetic?) conclusion. That this loss is a fairly recent event is attested by the fact that some monocotyledons do have a cambium layer in the bundles of their conservative parts. Thus the traces of the ordinary Indian corn show a cambium at the node. A bundle without a cambium is said to be *closed*, as opposed to one with a cambium, which is called *open*.

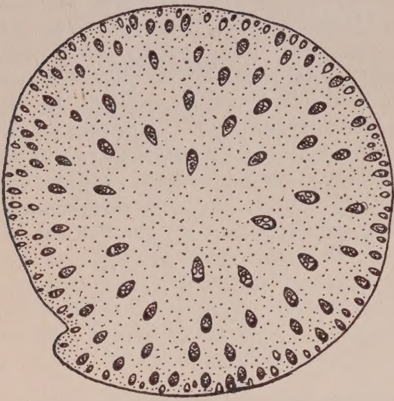

FIG. 124. — Cross-Sectional Diagram of Cornstalk Showing the Characteristic Distribution of Fibro-Vascular Bundles in Stems of Monocots.

In some monocotyledons the shortening of the internodes leads to a state in which the congestion of bundles becomes so great that as they enter the stem they begin to fuse with one another by their phloëm faces. This brings into existence a strand in which the xylem mass may come to enclose the phloëm completely, the result being a *closed concentric bundle.*

Monocotyledons are the most efficient of all herbs. They have attained the limit of reduction of conducting tissues. Their leaves are large, and their energies are devoted almost wholly to food manufacture. The remarkable part played by the grasses in the dietary of man rests upon their ability to manufacture great quantities of starch and to store it in their seeds.

Herbaceous stems have so largely dispensed with their supporting woody tissues that they have been forced to institute other means of strengthening their slenderness. This is usually accomplished by introducing sclerenchymatous tissue into the cortex in the form of a sheath beneath the epidermis or in the form of thick outer facings over the fibro-vascular bundles. Such stiffening tissues are distributed with admirable regard to the best architectural principles.

D. SUMMARY

The foregoing description of stem anatomy involving the pine, oak, linden, aster, buttercup, and maize, has, we know well, been detailed and difficult. Perhaps most of us will soon forget the facts which we have mastered with such pains. What, then, is the justification for the study?

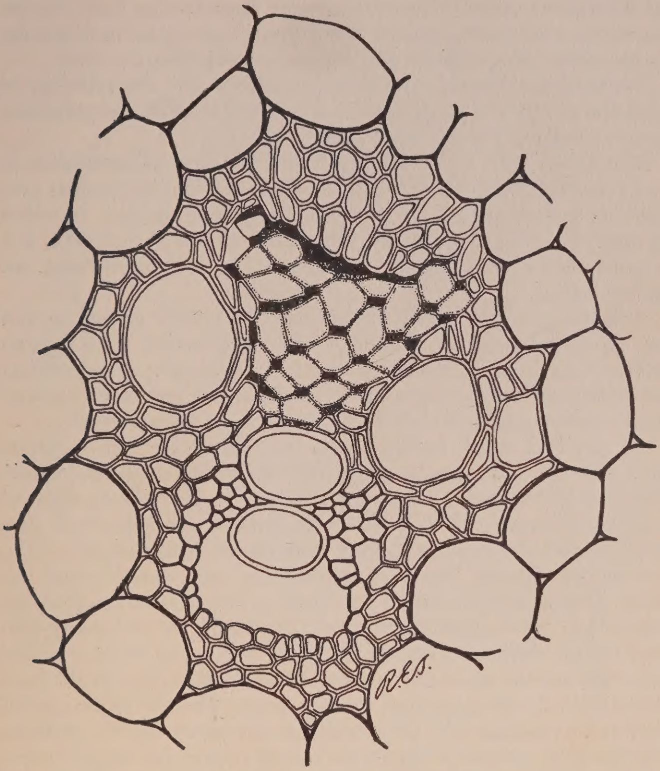

FIG. 125. — Cross-Section of a Single Fibro-Vascular Bundle of Corn Imbedded in Fundamental Tissue. The xylem is reduced essentially to four great vessels with accompanying fibers; the phloëm consists of sieve cells and companion cells as in buttercup. Cambium is totally extinct; hence there is neither secondary wood nor phloëm, and the bundle is "closed."

The purpose of education, as we have tried to point out before, is not to turn a student into an animated encyclopædia; it is rather to enhance and make subtler his powers of perception, and to lead him to see the broad, general principles which lie beneath facts and bind them into such coherence that they may become instruments of power which may be used in one's progressive conquest of the universe. Let no student make the serious mistake of neglecting facts, but let him realize that mere erudition is not enough; the truth he is seeking lies far deeper than sensuous perceptions and objective concepts.

We shall now see that the study of the anatomy and histology of stems has put us in a position to grasp some of the broadest principles which underlie the evolution of plants.

The woody tree, which attained a high state of differentiation in the Cretaceous Period, was the culmination of a long antecedent evolution no less remarkable than was its subsequent history. To follow the pre-Cretaceous story, however, is not practicable at this point. Let us rather see what surprising transformations took place after the Age of Chalk.

The tree is a culmination of ancient plant history carried on in a land of eternal summer. Compared with the modern herb it is an inefficient machine; it devotes too much of its energies to the production of a cumbersome mass of xylem which, after a few years, becomes almost useless, since it is transformed into the dead heart-wood.

As the cold which foreshadowed the coming Ice Age began to creep over the earth, the tree adapted itself to the changing weather conditions by improving its storage facilities. In the conifers, terminal wood parenchyma was evolved from septated tracheids and then slowly spread through the annual ring (diffuse parenchyma). The rays passed through stages of aggregation and compounding, till finally, forging steadily ahead and coming into association with the longitudinal wood-parenchyma, they developed the extremely efficient storage device around the incoming leaf-traces which we have called the leaf-ray and have interpreted as characteristic of the half-woody herb. In the meantime, to wage a more effective battle against the ever-encroaching cold, the stem began to assume the annual habit, and the plant withdrew its forces each autumn into subterranean winter quarters (herbaceous perennials), or else came to depend entirely on its seeds to carry on its life history (annuals). Running parallel to the perfection of the storage devices and the assumption of the annual habit, we can witness, too, a progressive perfection in physiological efficiency — the whole photosynthetic mechanism is being remarkably speeded up.

From another aspect the reduction of stelar tissues meant that the cambium layer was decreasing its activity and that there could be but the one orthogenetic (?) outcome which was finally realized in extreme herbs. For in the buttercup the cambium is breathing its last gasp; in the highly efficient monocotyledons the breath of life is extinct (though a few curious atavistic ghosts still persist in primitive forms). Since there is a limited amount of secondary tissue formed, or none at all, the primary phloëm and xylem have to be played up to carry on the necessary work of conduction between root, stem, and leaves. But the primary conducting tissues are meager, and consequently there is a necessity for more fibro-vascular bundles. Now if the bundles are to be increased in number, they can no longer keep up the circular alignment inherited from the ancient past.

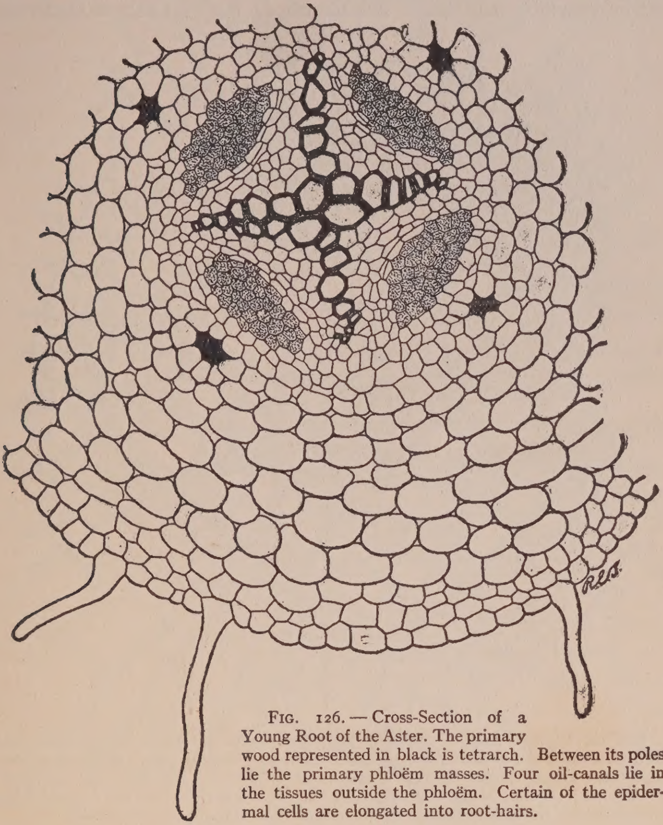

FIG. 126. — Cross-Section of a Young Root of the Aster. The primary wood represented in black is tetrarch. Between its poles lie the primary phloëm masses. Four oil-canals lie in the tissues outside the phloëm. Certain of the epidermal cells are elongated into root-hairs.

Hence there comes into existence the monocotyledon stem type with "the woody fibers distributed through . . . the cellular tissue."

From the foregoing summary we cannot fail to see that it is history again which unlocks the meaning of modern living things. Without the encroaching cold which culminated in the Pleistocene glaciation it is questionable whether herbaceous plants would have arisen at all. Without the herbs with their production of succulent stems and foliage and their edible fruits and seeds, the evolution of herbivorous mammals could hardly have taken place.

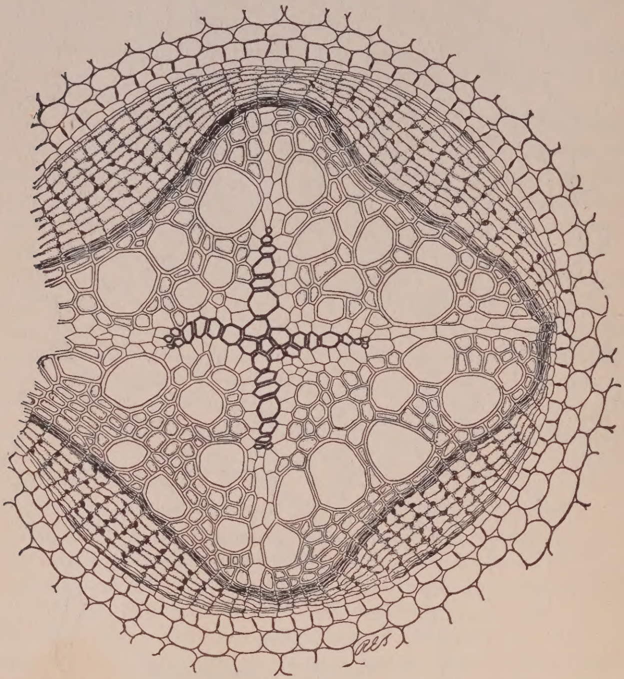

FIG. 127. — Older Root of the Aster in Cross-Section. Secondary wood is being laid down all around the circumference, but the cambium functions more vigorously at first beneath the primary phloëm masses. Opposite each protoxylem pole a ray has been built up. The pericycle just outside the phloëm is but one cell in thickness, and beyond it lies the endodermis, the radial cell walls of which bear thickenings (Caspary's bands).

The evolution of the herbaceous plant seems to bring us face to face once more with the doctrine of orthogenesis. Does it mean that

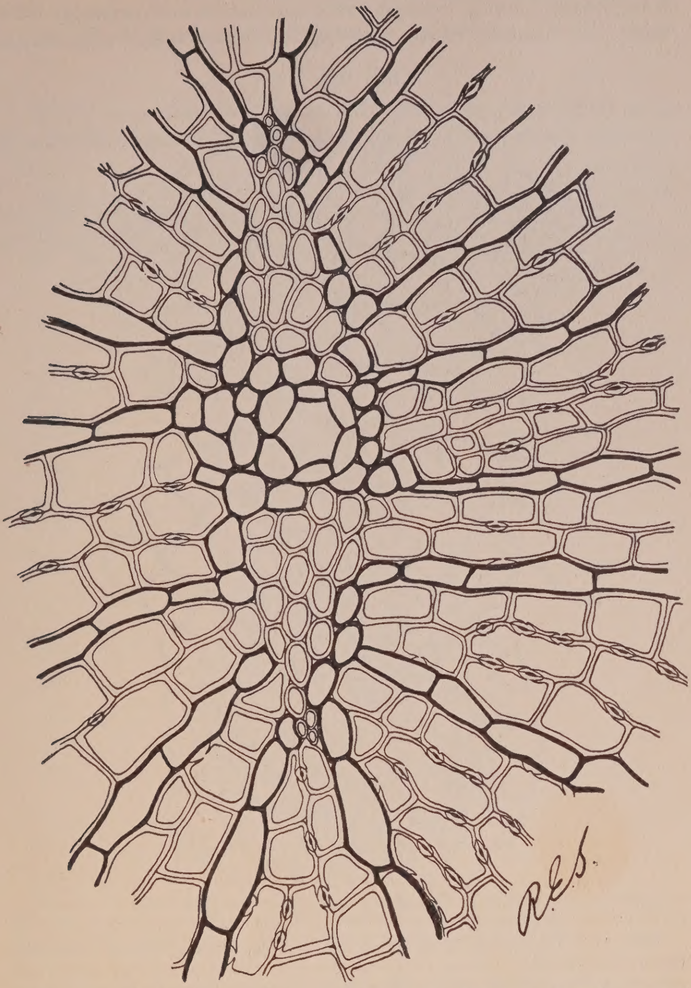

FIG. 128. — Cross-Section of the Central Part of a Hemlock Root. The primary wood mass is not darkened as in the preceding figures. It is diarch and contains a central large resin canal. Considerable parenchyma is associated with the primary wood.

Consciousness acting through evolution has been revealing or "creating" the Ideal Seed Plant as a sequential phenomenal story on our earth through 120 million years? Is this Ideal Seed Plant an organism with a definite morphology? Since authority seems to count for so much in modern science, we will show that this view is thoroughly

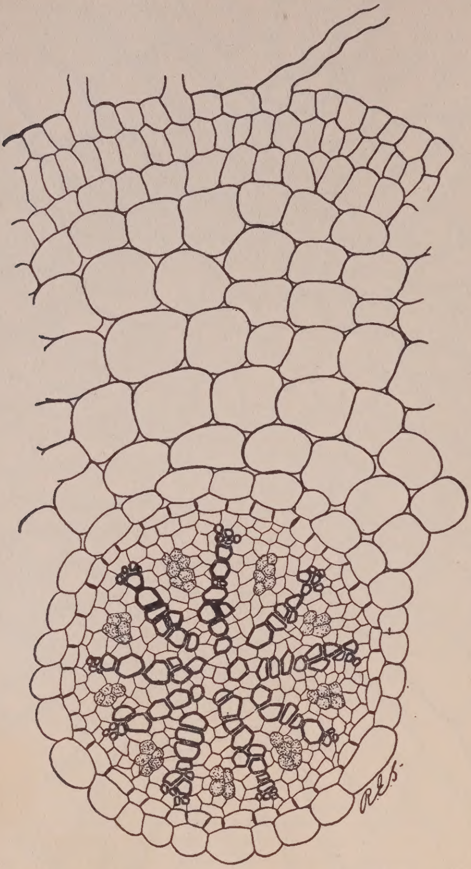

FIG. 129. — Cross-Section of an Orchid Root (*Pogonia*) Showing Typical Monocotyledonous Root Structure. The mass of primary wood is polyarch (or nonarch), and its poles alternate with small phloëm masses. The endodermis is well marked. Cortex and epidermis are shown above.

sane, sound, orthodox, and old-fashioned by stating that Plato would probably have interpreted it like that 2,300 years ago.

78. *The Root*

It will be recalled that the earliest conducting tissue which arises in a stem is of primary origin, that is, derived from primary meristem. In a cross-section of a young stem one would find a very thin ring of primary wood enclosing a pith and enclosed by a ring of phloëm and of cortex. Later, as we have learned, cambial activity starts up, and the wood and phloëm bands are widened by the addition of secondary tissue.

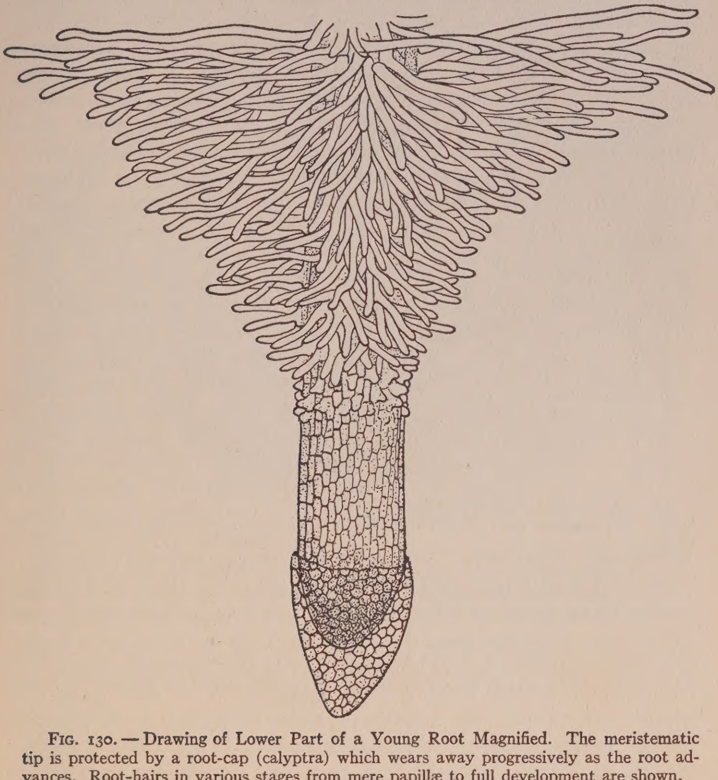

FIG. 130. — Drawing of Lower Part of a Young Root Magnified. The meristematic tip is protected by a root-cap (calyptra) which wears away progressively as the root advances. Root-hairs in various stages from mere papillæ to full development are shown.

The primary wood of a young root, however, forms a solid strand, and there usually is no pith at all (Fig. 126). This woody strand, too, is not usually circular in cross-section, but instead it is more commonly oval or star-shaped. The points of the oval or star are called *protoxylem poles*, and their number is expressed by terms such as *diarch*, *triarch*, *polyarch*, etc. It is to these poles that lateral roots are usually attached. Quite commonly they take their origin in the *pericycle*—a band of parenchymatous tissue just inside the endodermis—and bore their way out through the cortex. Hence, lateral roots are said to be *endogenous* in origin. Furthermore, the phloëm does not form a complete ring around the xylem but alternates with the poles or horns of the woody core. Because of the fact that the phloëm and the protoxylem poles lie on different radii, the young root is said to have *radial structure*.

If the root is of a kind that increases in thickness, the cambium layer starts first between phloëm and xylem in the spaces between the protoxylem poles and lays down secondary wood and phloëm. Finally the cambium extends its activity around the whole circle so that the later growth is hardly distinguishable from that of a stem (Figs. 127, 128). Many herbaceous plants and all monocotyledons are without secondary wood and phloëm in their roots; hence the primary radial structure remains evident and striking throughout life (Fig. 129).

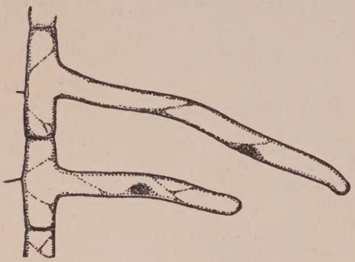

FIG. 131. — Two Root-Hairs Highly Magnified. The osmotic layer is the cytoplasmic utricle.

Correlated with its chief activity in the life of the plant, that of absorbing water and food salts, the young root is provided with certain appendages called *root-hairs* (Figs. 130, 131). If one germinates seeds in a moist chamber, it will be found that in the dark and humid atmosphere the delicate roots of the seedlings develop a dense plush of white hairs. Under the microscope these are found to be slender tubular prolongations of the epidermal cells. They can be traced through all stages of growth from their first appearance as delicate papillæ of the epidermal cells behind the root-tip to their final withering and disappearance. They are structures of only temporary activity and are continually being formed as the root-tip advances into new territory. It is sufficient here to note that the root-hairs are living epidermal cells with osmotic membranes of cytoplasm and that they are connected with the absorption of water and of food salts.

The epidermis, and consequently the root-hairs, are usually quickly lost from the root. This is due to the fact that a phellogen develops early and isolates the outer tissues, which soon die and scale off. Cork then forms the outer boundary of the root.

Another structure characteristic of the root is the *root-cap* or *calyptra* (Fig. 130), a thimble-like mass of cells which protects the delicate growing root-tip. The calyptra is ever being abraded away in front as it is pushed forward among the sharp soil particles, but it is constantly renewed behind by a definite meristematic layer called the *calyptrogen.*

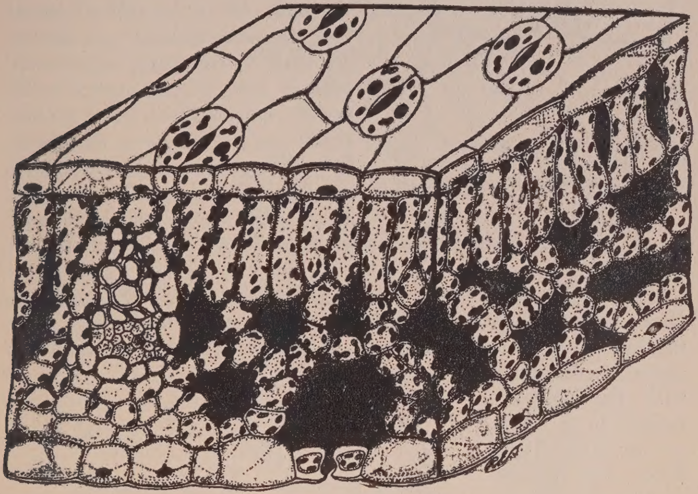

FIG. 132. — Sterodiagram of a Leaf Fragment. Both the upper and the lower epidermis bear stomata, shown in surface view above and in section below. The chlorenchyma or mesophyll is differentiated into palisade layer and spongy layer traversed by intercellular, gas-filled chambers (represented in black). At the left a small vein is represented in section.

79. *The Leaf*

The consideration of one last organ, the leaf, completes our study of the vegetative system of the seed plant. The leaf is the great food-manufacturing machine, and its motive power is sunlight. It is a kind of sun-engine, and its shape and anatomy are expressions of the fact. The accompanying stereodiagram, Fig. 132, is to be compared with the following description.

The leaf is covered with a layer of colorless, flattened, epidermal cells, part of which are differentiated to form odd structures called *stomata* (singular, *stoma*). Each stoma consists of a small slit-like opening bounded on either side by a crescent-shaped *guard cell* whose activities regulate the size of the opening (Fig. 133). The stomata are the pores through which gases enter and leave the inner parts of the leaf. On dorso-ventral leaves they are more abundant on the under than on the upper surface and average 100–300 per square millimeter. Leaves which stand up vertically, such as those of the yucca, iris, and grass, are provided with stomata about equally on both sides, while leaves which float on water, such as those of a water lily, have them only on the upper side.

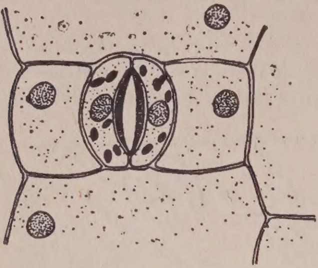

Fig. 133. — Single Stoma in Surface View. Guard cells with chloroplasts enclose the stomatal slit and regulate its opening.

On many leaves the epidermis is beset with hairs, as is also the stem. Hairs are variously shaped epidermal outgrowths, sometimes mere papillæ of the cells, in which case they resemble fine velvet; or again multicellular with the cells arranged in a single row or massed into larger and thicker bodies, often of peculiar and distinctive shapes (Fig. 135). In some plants the hairs have swollen and glandular tips and produce resinous or gummy secretions. A distinction may be drawn between hairs and emergences. *Hairs* are distinctly epidermal products; *emergences* involve not

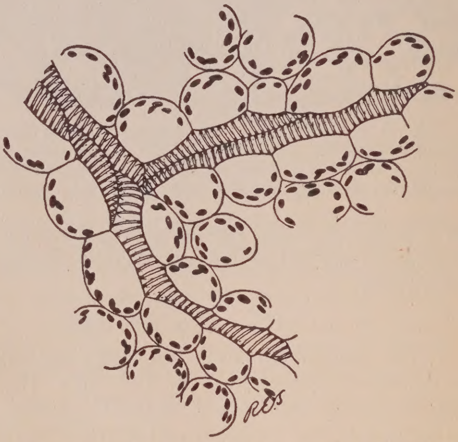

Fig. 134. — Terminus of a Vein in the Leaf of Wild Cucumber (*Echinocystis lobata*). The phloëm of the vein has dwindled away; spiral tracheids conduct water and salts to the chlorenchyma cells.

only epidermal cells but deeper-lying tissues as well. Prickles are usually emergences.

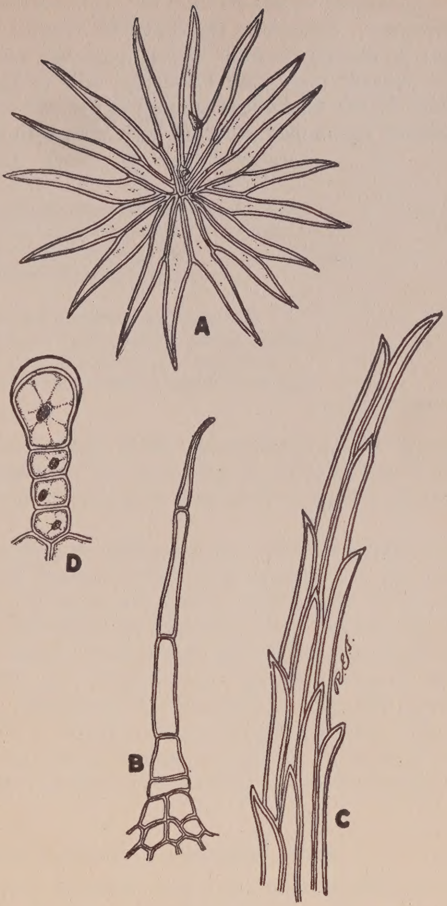

Fig. 135.—Hairs from Various Plants: A, stellate hair from the leaf of *Eleagnus umbellatus;* B, hair from a sunflower leaf; C, pappus bristle from achene of aster; D, glandular hair from a pelargonium leaf.

The inner structure of a typical dorso-ventral leaf is definitely related to its function as an engine for food-making. It uses the sun as a motive force. Between the epidermal layers lies a sheet of chlorenchyma technically called the *mesophyll.* It is differentiated into an upper and a lower layer of cells. The cells of the upper layer are elongated perpendicularly to the surface; they might be compared to myriads of cylinders set on end. This constitutes the *palisade layer.* Beneath the palisades is another layer of mesophyll which is traversed by a system of intercellular air spaces. It is called the *spongy parenchyma* and into its air chambers open the stomata so liberally scattered over the lower epidermis. The whole leaf, too, is traversed by veins and veinlets, which, at the same time, form a supporting framework and provide a conducting system for raw materials and for manufactured products (Fig. 134).

Ecological variations from the typical structure just described are numerous. Sometimes the epidermis consists of multiple layers and may be utilized for water storage (e.g., the mangrove). In sun leaves the palisade layer may be several cells in thickness as opposed to shade leaves, where it is reduced to one cell layer. In upright leaves palisade layers may occur on both sides with spongy tissue between.

CHAPTER XIII

COAL AND ITS FORMATION

"There rolls the deep where grew the tree.
  O earth what changes hast thou seen!
  There where the long street roars, hath been
The stillness of the central sea.

The hills are shadows, and they flow
  From form to form and nothing stands;
  They melt like mists, the solid lands,
Like clouds they shape themselves and go."

— TENNYSON.

We have completed a study of the vegetative system of the seed plant and are equipped with the knowledge requisite to take up the interesting problems which have to do with the functions of this wonderful plant machine.

At this point, however, we shall digress to consider a subject not commonly taken up in elementary botanical courses, but one which is of the utmost importance to our present civilization. This is the study of coal and the method of its formation. It is both a botanical and a geological subject and serves to show the student that our formal sciences are man-made conventions; nature herself knows no sharp limits between them. The reason for introducing coal at this point in our course is that coal is largely composed of plant debris — the remains of the vegetative system of plants — though, as we shall soon see, certain parts of the reproductive system also play a curious part in coal formation.

80. *The Divisions of Geological Time*

From time to time in our past work it has been necessary to use terms referring to the divisions of geological time. The writer has realized that unless the student has had some work in historical geology these terms could carry little meaning. But now that we are to study a subject which stands on the border-line between botany and geology, they must be understood, and so it seems desirable to introduce a table of the main time divisions of the earth's history. This will give the student some idea of the position of the Coal Period. The chronological notes are introduced to assist the memory in associating the periods with definite events. It is realized that some of these carry little significance at this stage of the student's study. The table should, however, be a useful one for reference later on. The arrangement of the periods is in the order of the superposition of the rocks, with the oldest ones at the bottom and younger ones at the top.

ERA	PERIOD	TIME SCALE IN MILLIONS OF YEARS		CHRONOLOGICAL NOTES
		Minimum	*Maximum*	
PSYCHOZOIC	2. Recent	1	1.5	Man; increasing dominance of herbaceous angiosperms.
	1. Pleistocene			Glaciation; primitive man; wide extinction of plants.
CENOZOIC	5. Pliocene	7	9	
	4. Miocene	19	23	Himalayas rise; man-apes. Modernization of plants.
	3. Oligocene	35	39	Pyrenees and Apennines rise. Retreat of polar floras.
	2. Eocene	55	65	Modern mammals, four-toed horses. Also primitive mammals and five-toed horses. North American lignites; dominance of sequoias. Tropical flora still in Arctic regions.
	1. Paleocene			
MESOZOIC	4. Cretaceous	95	115	Andes and Rockies rise. Modern tropical plant families within Arctic Circle.
	3. Comanchean	120	150	First flowering plants — *Prepinus*, *Pinus*, and araucarians.
	2. Jurassic	155	195	Sierras rise; pterodactyls and birds; primitive reptile-like mammals. Angiospermous *Caytoniales*.
	1. Triassic	190	240	Dinosaurs and dominance of cycadophytes; primitive conifers and ginkgos.

Era	Period	Time Scale in Millions of Years		Chronological Notes
		Minimum	*Maximum*	
Paleozoic	7. Permian	215	280	Appalachians and Urals rise.
	6. Pennsylvanian	250	330	Paleozoic Alps; primitive insects; eastern American coal deposits. *Lepidodendrons*, *Calamites*, *Primofilices*, *Cycadofilicales*, *Cordaitales*.
	5. Mississippian	300	370	Early coal deposits.
	4. Devonian	350	420	Earliest known land plants: *Psilophytales*, primitive *Lycopsida* and *Pteropsida*.
	3. Silurian	390	460	Fishes.
	2. Ordovician	480	590	Rise of invertebrates.
	1. Cambrian	550	700	Dominance of trilobites.
Proterozoic	Late		1,000	*Protozoa*, simple *Metazoa;* bacteria and algæ.
	Early		1,200	
ARCHEOZOIC, PALEO-LAURENTIAN, ETC.			(1,500)	
PRIMORDIAL				
COSMOLOGIC			(3,000?)	Origin of the earth.

As can be seen from this table, the coal-fields of Pennsylvania and Ohio are variously estimated to be between 250 and 330 millions of years old. This means, in a certain sense, that the coal which glows in our grates is setting free the sunlight which fell on an ancient forest some 300 million years ago.

81. *Theories and Facts about Coal Formation*

The term *coal* is applied to a rather wide variety of carbonaceous material which is wholly of organic origin, though the generally taught and accepted theory that it was derived from peat-bogs is open to serious question. This is the *autochthonous* theory of coal formation — the idea behind the word being that the coal was formed in the places where the trees grew.

Opposed to the autochthonous theory is another which seems to have been proved almost beyond question.* The vast majority of coal deposits represent masses of transported vegetable material which was swept by rivers into open water. This constitutes the *allochthonous* theory, and the word implies that the material was brought from a distance and that the coal was not formed *in situ*. Therefore, instead of studying the peat-bog as an illustration of the initial stages of coal formation, we study to-day the deposits of muck which are accumulating in bodies of quiet water. In their sequence of deposition and in their microscopic characters they display a striking similarity to the same features as exhibited in coal-beds.

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* E. C. Jeffrey, "The Origin and Organization of Coal," *Mem. Amer. Acad. of Arts and Sci.*, XV, No. 1, 1924.

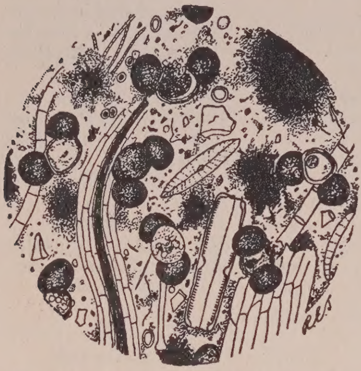


FIG. 136. — Fine Pond Muck with Pine Pollen, Plant Debris, and Inorganic Matter.

Pond muck consists of comminuted vegetable debris, and like coal it is often singularly free from inorganic material. If a small portion be examined with the microscope, the trained vegetable histologist will recognize fragments of roots, stems, and bark along with remains of microscopic water plants and of animals. Another very conspicuous feature demands emphasis. Almost every slide of pond muck derived from temperate climates is full of pollen grains. These come mostly from the pine or from other coniferous trees. The pines and their allies are wind-pollinated, and to facilitate dispersal their pollen grains are provided with two bladdery, air-filled wings. Hence they may be transported for long distances. The following quotation vividly illustrates the efficiency of their distribution devices:

> "Two lightships stationed respectively 18½ and 33 miles from land were fitted up with sticky plates exposed to the air. Examination later disclosed the fact that there were adhering to each square inch of the plate on the first ship 4,500,000 grains of spruce pollen, almost as many birch pollen grains and one-third as many pine pollen grains. The plate on the ship farthest out showed about one-half of these quantities."

In spring the dwellers in the country sometimes speak of "showers of sulphur" which accumulate on quiet ponds. The "sulphur" consists of myriads of pollen grains largely derived from coniferous trees. They drift for a time into eddies and windrows on the water, then finally sink and are added to the muck beneath. Thoreau says in *Walden* under the essay entitled "Spring": "The sulphur-like pollen of the pitch pine soon covered the pond and the stones and rotten wood along the shore, so that you could have collected a barrel-ful. This is the 'sulphur-showers' we read of." Such are the conditions under which fresh-water muck is accumulating to-day, and pollen makes up no small part of the vegetable debris.

Fig. 136 is a drawing of a bit of fine pond muck as seen under the microscope. Pollen grains, fragments of plant debris, and masses of colloidal and amorphous organic matter appear. The latter is an accumulation of organic dust held in a mucous matrix derived from plants and animals; much of it is probably the excrement of worms, crustacea, etc.

In order to study the constituents of coarser muck more intimately, small masses of it may be tied up in cheesecloth, imbedded in celloidin and cut into thin sections. Fig. 137 is drawn from a microscope slide prepared in this way. Sections of pollen grains, pine wood, roots and a pine needle are visible.

Such relatively fine material is not, however, the only constituent which enters into coal. During times of high water the larger rivers flowing into lake or sea sweep up abundant forest litter ranging in size all the way from twigs and leaves to branches and great tree-trunks. These, too, will be added to the muck deposit. It is evident that where the lands are heavily forested and where there are seasons of heavy rainfall, such coarse woody debris will far preponderate and will stamp the deposit with a definite woody character wherein the finer waste plays but a subordinate part. The writer has seen the Oregon shore heaped high with driftwood made up of giant contorted roots, and skeleton trunks and branches splintered and crushed like matchwood by the terrific force of the winter storms. Vast quantities of such material must become water-logged and sink off shore. As the ages pass, it will be covered with sediments and yielding to the enormous pressure will be converted into what is called *brown coal* or *lignite*.

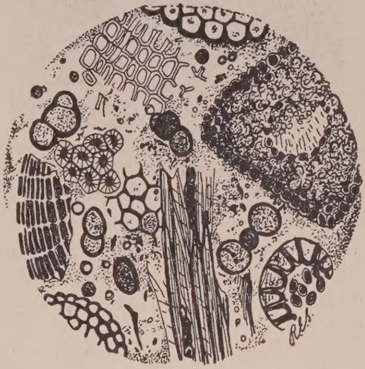


FIG. 137.—Section of Coarse Pond Muck. Based on a slide prepared from muck derived from a lake near Little Metis, P. Q., Canada, and furnished by Professor E. C. Jeffrey.

This term is applied to deposits of carbonaceous material largely made up of wood and so little changed that it still displays clear evidence of its derivation in the flattened trunks and branches scattered through it. Some of these were charred in ancient forest fires and their structure is so well preserved that they can be easily sectioned and referred to the kinds of trees from which they came. Fig. 138 is drawn from a prepared slide of a Texas lignitic wood. The tree had been scorched, and our section is taken at the junction point to which the influence of the heat has penetrated. The charred and brittle tracheids below have broken under the pressure of the overlying sediments, but the tracheids above were swollen with water and have collapsed under the pressure into a body in which the constituent cells are still dimly visible. At a stage beyond this they would flow into a structureless brown mass.

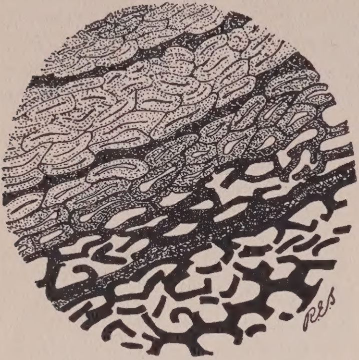


Fig. 138. — Section of a Charred Fragment of *Brachyoxylon* Wood from Texas Comanchean Deposits.

The United States is well provided with brown coal deposits. The Great Interior Coal Field runs from northern Mexico into Canada, a distance of nearly 2,300 miles, and has an east and west extension from the 103d to the 115th meridian, nearly 1,200 miles. This includes the states of the Great Basin region. Most of this lignite belongs to the relatively modern Tertiary (Paleocene) deposits. We know that the Great Basin was then being drained of a deep inland sea which had lain over it during the Cretaceous Period. Forests luxuriated along the coastal lands and their fallen leaves, fruits, trunks, branches, and uprooted stumps were swept into shallow water and piled up in confusion to be slowly converted into lignite.

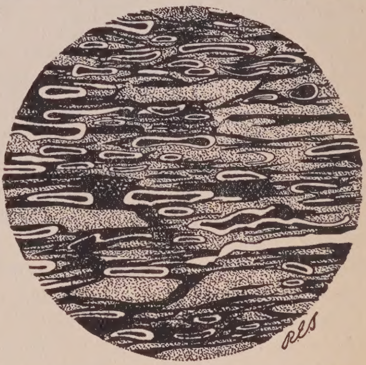


Fig. 139. — Section of Cannel Coal Cut Perpendicularly to Bedding Planes. Based on a slide prepared from specimen derived from Blue Grass, Ky., and furnished by Professor E. C. Jeffrey.

The more ordinary coals, however, including cannel, bituminous, and anthracite, belong to much older geological horizons and have become so compacted and hardened that their preparation for microscopic study involves great technical difficulty. Only recently have these difficulties been overcome. Formerly the sections were sawed out of blocks of material by the use of lapidary's instruments, ground as thin as possible on an emery wheel, and then polished with diamond dust. This method at its best produces sections too thick to show very much structure. To-day, however, the hardest anthracite can be sectioned in an ordinary slide microtome. The method of preparation consists of prolonged treatment with hydrofluoric acid and a final imbedding in celloidin forced into the coal under pressure.

82. *Cannel Coal*

It has always been admitted, and even by disciples of the peat-bog theory of coal formation, that cannel coal was formed from drift material in open water. It occurs in lens-shaped beds which evidence the shape of the old lake basins where they accumulated. It sometimes contains fossils of fresh-water fish. Cannel coal is dull in color; it burns with a bright white flame and leaves little ash. It is a superior coal for grates, but the supply is becoming limited.

When a slide of cannel coal cut perpendicularly to the bedding planes (Fig. 139) is placed beneath the microscope, a striking and brilliant display of color appears. Through a brownish matrix streaked with black and deeper brown are sown myriads of loop-shaped, bright yellow bodies all lying in the same plane. They vary somewhat in size, but among them certain very large ones are often visible. These bodies are all flattened spores (essentially pollen grains) shed from the trees of the Coal Period, and shed in such remarkable abundance that they form the most conspicuous part of certain coals. They were drifted into ancient watercourses just like modern showers of sulphur. The brownish matrix with which the spores are compacted is obviously woody debris pressed into a state where its cells have flowed into a homogeneous mass. Yet with a little search one can often find all stages in the compacting process from fragments of wood, with their border-pitted tracheids and rays well preserved, to a final state where the material is wholly amorphous. Often, too, bits of charcoal are found in the sections. Such must represent the debris from burned forests. Forest fires could not have been rare in lands where volcanoes were often active and where thunder-storms occurred.

83. *Bituminous Coal*

Let us now examine a section of bituminous coal and compare it with cannel. To the naked eye a fresh surface broken across the bedding planes displays alternating gleaming and dull bands. Miners call the bright stripes "glance coal," while they speak of the dull ones as "mat coal."

Under the microscope it at once becomes evident that the glance areas consist of amorphous wood; each band represents a trunk or a branch or a twig mashed to a jelly (Fig. 140). The dull stripes have exactly the appearance of cannel coal and were formed in the very same way from compacted spores and fine vegetable matter. The mat coal, then, may be called *canneloid*, as opposed to the woody bands which are denominated *lignitoid*. Bituminous coal differs from cannel only in the fact that it contains more wood and may have been deposited in brackish or salt water rather than in fresh. Very probably the canneloid layers were deposited in times of quiet, sluggish water, while the trunks and other woody matter which compose the glance or lignitoid areas were transported by violent streams after severe storms. We realize that a similar sorting process goes on to-day where running water enters quiet ponds or lakes. Now if cannel coal was formed from materials transported by running water, we cannot deny the same method of formation to bituminous coal, which has the same structure. The peat-bog theory was based on insufficient evidence.

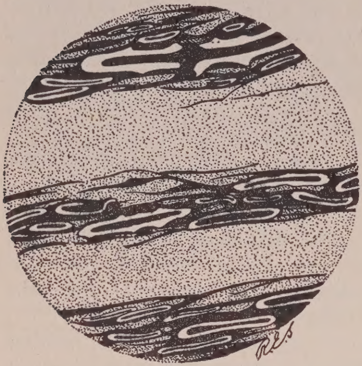


FIG. 140. — Section of Bituminous Coal Cut Perpendicularly to Bedding Planes. Based on a slide prepared from specimen derived from Dunfermline, Scotland, and furnished by Professor E. C. Jeffrey.

Anthracite has essentially the same structure as has bituminous coal, but owing to the great changes it has suffered it is less well preserved.

84. *The Ancient Coal Swamp*

The plants which entered into the formation of the great coal-beds of the Carboniferous Period were quite different from any living to-day. Around the low shores of the inland sea which washed over Tennessee, Pennsylvania, and Ohio stood forests composed of somber trees. They belong to orders long ago extinct or now dwindled to a few insignificant relatives. The modern trivial club-mosses were represented by the giant lepidodendrons and sigillarias, which towered to a hundred feet and bore great cones which must almost constantly have filled the air with drifting clouds of spores. They were fastened to the earth by rhizome-like bases (*Stigmaria*) which ran through the mud in all directions.

Scrambling over the lepidodendrons and interspersed among them were archaic ferns and fern-like seed plants, the latter being the most remarkable group which paleobotany has yet discovered, and constituting a link between ferns and gymnosperms. Our degenerate *Equisetum* was represented by its ancestral dendroid race of calamites which bore a somewhat superficial resemblance to giant bamboos. The waters were filled with algæ, while animal life was represented by hosts of invertebrates such as molluscs, crustacea, and worms. Primitive insects flew among the trees, though since there were no flowering plants the *Lepidoptera* were not represented. Archaic fishes swarmed in the sea and had already given rise to their strange amphibian descendants, the *Stegocephalia*, which were crawling along the muddy shores. There were as yet no birds or mammals, though a few reptiles were present.

Such was the world in which the deposits of vegetation were formed which were to be solidified into coal and sent down the ages to make possible a twentieth-century civilization.

CHAPTER XIV

THE PHYSIOLOGY OF THE VEGETATIVE SYSTEM

In the last chapter we plunged back into the abysses of geological time and caught a hasty glimpse of the world in which coal was formed. We must return from that digression and resume the study of the plant machine. We know it fairly well as a static body and are in a position now to understand its activities. The logical point to begin the study of the physiology of the vegetative system is with the function of nutrition, and for this the study of the cell has already prepared the way. We shall first learn how the plant makes food for itself, how it stores and transports it, and finally through katabolic changes breaks it down to simpler compounds, thereby utilizing the energy contained for further chemical and physical activities.

A certain group of chemical elements is yielded by the plant when it is analyzed. Certain of these are merely accidental derivatives from the soil, but a group of ten is absolutely essential for normal nutrition and growth. These are carbon, hydrogen, oxygen, phosphorus, potassium, nitrogen, sulphur, calcium, iron, and magnesium. Plants can be grown to full fruiting maturity with their roots in distilled water if compounds containing all these elements, except carbon, be dissolved in it. The formula for such a nutrient solution (Knop's solution) is:

Water	1,000 cc.
Calcium nitrate	1 g.
Magnesium sulphate	0.25 g.
Potassium nitrate	0.25 g.
Acid potassium phosphate	0.25 g.
Ferric chloride	trace

We may now consider in more detail the entrance and subsequent use of these essential elements and compounds.

85. *The Movement of Water through the Plant*

Plant chemistry is a water chemistry; chemical activities go on in vacuoles filled with dilute water solutions; water makes up a high percentage of the protoplasm of the cells; it saturates the cell walls and serves as a medium both for osmotic activities and for active mechanical translation of salts.

Water enters through the root-hairs with which the young growing parts of roots are liberally provided. It moves by osmosis to the cortical cells and is finally exuded into the tracheids or vessels of the xylem. This last step is not easy to explain. Neither tracheids nor vessels possess protoplasm, and hence the ingress of water cannot be due to osmosis. We only know that the turgor pressure rises very high in the cells adjoining the xylem and that finally water begins to be forced through the cellulose walls of the cortical cells into the adjoining woody elements, when it begins to rise into the stem. The turgor pressure of the living root cells can be measured by attaching a glass manometer to a root stump and observing the height to which the exuding sap can force a column of water or mercury. It has been found that the pressure is sufficient to raise a column of water to a height of twenty, twenty-six, or exceptionally to sixty feet (in birch). The amount of water flowing from such a severed stump varies considerably with different plants. In the grape, one quart per day may be given out; in the birch, 5.2 quarts; in the palm, some sixteen quarts. This is not absolutely pure water, but contains traces of the salts which were dissolved from the soil.

Turgor pressure of the living cells of the root is called *root pressure*, and it is evidently a sufficient force to start the stream of sap on its way to the leaves. Yet it is not enough to account for the full ascent of sap to the tops of the tallest trees, since some of these, like the sequoia, rise to a height of 300 feet. Other factors must be invoked to account for this phenomenon. It must be confessed that botanists do not yet know how water can be carried to such heights. The participation of the leaves is probably necessary to the process and a recent theory (Joly-Dixon) places great weight on this factor. Before we can understand the theory, however, it will be necessary to follow the ascending stream of water to its destination.

The metabolic activities of the plant demand no such quantities of water as actually enter through the roots. Most of it is destined to be evaporated into the air through the leaves. As water rises in the sap-wood, passing from tracheid to tracheid through the bordered pits, a small part of it is carried to pith, phloëm, and cortex to supply these tissues with the water necessary to their activities, but the great bulk ascends through the leaf-traces and enters the leaves. Here it is conducted through veins and veinlets in a manner somewhat analogous to the way in which distributaries of a river run over a delta. Up to this point the water channel has been an open conduit, but the veinlets come to blind termini grading away into elongated, closed parenchyma cells where osmosis starts up once more. The living cells actively absorb water through their protoplasmic membranes into their inner vacuoles, and as a consequence their turgor pressure rises and the leaf tissue becomes firm.

86. *Transpiration*

All wet bodies when exposed to air lose water from themselves by evaporation. We have learned that the leaf is traversed by a rich system of intercellular air spaces which open to the exterior atmosphere through the epidermal stomata. Consequently there is continual evaporation from the parenchyma cells into the intercellular spaces and thence outward through the millions of stomata. This process of water loss is called *transpiration.*

It is not exact to think of transpiration as going on in quite the mechanical way just outlined. The stomata with their guard cells act as regulatory valves whose activities are controlled by light and atmospheric moisture. When turgid with water they expand in such a manner as to widen the stomatal opening. On the contrary, when they are flaccid, the guard cells shrink together and the slit is closed. The movement of the guard cells is intimately related to the fact that they alone of all the epidermal cells possess chloroplasts. This permits them to manufacture sugars when light falls on them. Then as the osmotically active solute increases, water from adjacent cells begins to enter, the guard cells swell, and as a consequence the stomatal slit is widened.

The Joly-Dixon theory of the ascent of sap is based on the obvious fact of transpiration. In broad outlines it states that water is dragged upward from the root by the force of transpiration. This necessitates the assumption that columns or threads of water even 300 feet long will be held together by the cohesive force of the molecules and adhesion to the walls of the conducting cells. Physical experiments have really shown that this force is sufficient to support such long columns. One objection urged against the theory is that since bubbles of rarefied air occur in the tracheids and vessels, the water columns must necessarily be broken from time to time. If this actually happens, it is difficult to see how they could be reformed. There is no necessity, however, for the water thread to pursue a perfectly vertical course. If it strikes a tracheid with an air bubble, it may be deflected horizontally through a bordered pit to an adjoining water-filled tracheid and thus its continuity would not be interrupted. The structure of the membrane in the bordered pit and the peculiar method in which the torus is deflected to block up the mouth of the pit in an air-filled tracheid would seem to be a provision to prevent the spread of air bubbles. Whatever may be the final explanation of the ascent of sap, the Joly-Dixon theory to-day seems to have most to recommend it. In passing, it may be mentioned that the Hindu physiologist Bose maintains that water is pumped up the tree by an actual rhythmical contraction and expansion of the utricles of the living cells after the analogy of a multitude of pulsating hearts.

If we ask why water rises through the plant in such quantities only to be transpired through the leaves, the answer is that the process serves to condense the nutrient salts brought up from the soil to a concentration conducive to better metabolic activity. Osmosis alone, though it serves well enough in low thallophytes, is altogether too slow a method of transporting water in tall land plants, hence the fibrovascular system has been devised to provide for a direct "transportation current" of water which sweeps salts along as a river sweeps suspended silt.

The amount of water-vapor passing from the leaves by ordinary transpiration is extremely large. In summer time the amount discharged from the plant each day probably equals its weight. It has been estimated that an oak with 700,000 leaves transpired 244,695 pounds of water (about 29,500 gallons) between June and October. A birch with 200,000 leaves transpired 700 to 900 gallons per day during a hot summer season. This means that one acre of such trees would throw into the air in the course of a season 3,168,000 pounds of water. It is estimated that an acre of grass transpires about six and a half tons of water on a single hot summer day. It is little wonder, when one considers such figures, that plants are constantly menaced by drought during the growing season and that they have taken on so many protective devices to reduce the rate of water loss.

In some cases water is actually exuded from the plant in the liquid form. On summer mornings after a warm night it is not uncommon to find the edges of the leaves of the garden nasturtium (*Tropæolum*) beset with droplets of water. This is usually ascribed to "dew," but it is water which has actually come from the veins of the leaf. The leaves of Indian corn throw out liquid water in a similar manner under the same conditions. In some tropical plants water is discharged in considerable quantities. A single leaf of one of the tropical arums may excrete 0.1 quart of water during the night.

Why is it that with the constant menace of death from desiccation the stomata remain wide open and permit the process of transpiration to continue to the danger point and beyond? It has already been pointed out that the stomatal movements are regulated by light. The stomata must be kept open, not primarily to provide for transpiration, but to permit the ingress of carbon dioxide for the subsequent process of starch manufacture. This fact forms a natural transition to the subject of photosynthesis, which is undoubtedly the most important single subject that the science of plant physiology has to teach.

87. *Photosynthesis*

If one asks the layman whence a plant derives its food, the answer will usually be that food comes from the soil. Yet this is scarcely true in any sense. Neither animals nor plants can live on inorganic chemical salts and water. Both must have proteids, carbohydrates, and hydrocarbon foods. The only real difference between the nutritional processes of plants and animals is that the former can manufacture their own foods from raw materials, while the latter cannot. The chemical salts which enter through the root-hairs and ascend with the transpiration current are not plant foods; they are merely the materials from which plant foods are to be manufactured.

Even if we admit that the salts do constitute plant food, we should realize that fully 50 per cent of the plant body is composed of carbon which comes not from the soil but from the air.

Photosynthesis — a word which means "putting together by means of light" — is the term applied to the process of carbohydrate manufacture by green plants. It may be defined as an anabolic process in which carbon dioxide and water are synthesized to carbohydrates under the influence of chlorophyll and light, while a certain amount of oxygen is set free as a waste product. The activity may be represented in a simple and quasi-chemical reaction as follows, though it should be distinctly realized that the molecular proportions here set down do not represent the actual ones:

$$6CO_2 + 6H_2O \text{ under influence of chlorophyll and light} \rightarrow \underset{\text{sugar}}{C_6H_{12}O_6} + 6O_2.$$

A. CARBON DIOXIDE

When the theory was first propounded that the carbon dioxide gas of the air is the source of the carbon of the plant body, it met with violent opposition from those who contended that the soil humus was the source of the element. Yet the possibility of growing plants to maturity in carbon-free water or sand cultures showed conclusively that the carbon of the plant did not enter through the roots. This statement must not be considered as absolute; it is known to-day that certain carbon-containing compounds may be absorbed through the roots of plants, though this does not affect the fact that the major source of supply is the atmosphere. The average amount of carbon dioxide in the air is about 2.8 parts in 10,000. This means that there are some two grams of carbon in 10,000 liters of air. In order for a single tree having a dry weight of 11,000 pounds to acquire its 5,500 pounds of carbon, it must deprive 15,696,000 cubic yards of air of their carbon dioxide. With such stupendous figures confronting them it is small wonder that the early plant physiologists were slow in accepting the fact of photosynthesis.

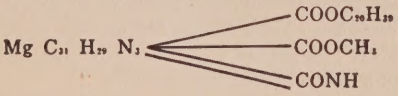
It would almost seem that the atmosphere should have been long ago depleted of its carbon dioxide gas; yet we must realize that all processes of organic fermentation and decomposition restore it to the air, while the respiratory activities of plants and animals as well as the gases from millions of manufacturing plants contribute to the amount. The reverse question may occur: If vegetation has not increased on the earth, why has not the present tremendous consumption of coal produced an excess of carbon dioxide in the atmosphere — so much in fact that it might become deleterious to animal life? It is believed that the ocean acts as a regulator of atmospheric gases. As the partial pressure of any gas increases, it is absorbed in proportionately greater quantities, and consequently the composition of the air remains practically constant.

B. CHLOROPHYLL

Up to 1912 our knowledge concerning chlorophyll was rather slight. It was known to be a green pigment held in the chloroplast. It was found to be soluble in hot alcohol, in ether, benzine, carbon tetrachloride, etc. In transmitted light it was seen to be green, whereas light reflected from its surface was blood-red.

In 1912, the German chemist, Willstätter, and his students began to publish on the chemical structure of chlorophyll and to-day we know not only its structure but also its decomposition products in considerable detail. First of all there are two chlorophylls, called by Willstätter chlorophyll *a* and chlorophyll *b*. The former crystallizes to a blue-black solid and forms a dark green solution; the latter is dark green in the solid form and bright green in solution. In land plants the proportion of chlorophyll *a* to chlorophyll *b* is about 3:1. The two chlorophylls are very similar in structure. Chlorophyll *a* is $C_{55}H_{72}O_5N_4Mg$, while chlorophyll *b* is $C_{55}H_{70}O_6N_4Mg$. They are both essentially fats or esters of a tribasic acid, chlorophyllin, and a peculiar alcohol, phytol.

The structural formula of chlorophyll *a* is:



$$\mathrm{Mg\ C_{31}\ H_{29}\ N_3} \begin{cases} \mathrm{COOC_{20}H_{39}} \\ \mathrm{COOCH_3} \\ \mathrm{CONH} \end{cases}$$

Here we have the magnesium-containing acid with its three substituted carboxyl groups. One hydrogen atom is replaced by phytyl

($C_{20}H_{39}$), another by methyl (CH_3), while the third represents what is called the "lactam arrangement" (CONH).

Chlorophyll is also associated in all plants with two yellowish pigments, *xanthophyll* and *carotin.* Xanthophyll is an oxide of carotin, and its derivatives or allied compounds are responsible for the yellowing of autumn leaves. Carotin takes its name from the carrot, to which it imparts the orange color. It is soluble in chloroform, ether, or carbon disulphide and can be crystallized out in the form of orange-red plates. Its chemical formula is $C_{40}H_{56}$.

Returning to the subject of chlorophyll, there is another fact of peculiar significance to be noted concerning it. It is easily decomposed by acids or alkalis till finally a residue, *hemopyrroie,* is obtained which is precisely the same structural compound that is finally derived from the decomposition of the red blood pigment — *hematin.* In other words, hematin and chlorophyll are formed from the same mother substance. In the former, the metallic element involved is iron; in the latter, it is magnesium.

It will be evident to the student that plants without chlorophyll, such as the Indian-pipe, coral-root, the balanophoras, and the host of mushrooms and other fungi, are totally unable to carry on photosynthesis. Since they cannot make their own food, they are forced to assume parasitic or saprophytic habits and to dissolve their food from the substratum by means of secreted enzymes.

C. LIGHT

Photosynthesis is usually considered to depend upon sunlight. This is not strictly true, since artificial light such as that from an arc-lamp will also serve as the source of energy. It is astonishing what a small amount of light is sufficient to start the process in certain plants. If a lighted match be held for one second ten centimeters away from the small green algal cell *Chlorella,* photosynthesis starts up and the evolution of oxygen can be detected. Moonlight is also sufficiently powerful to keep up the process in certain algæ.

The effect of absence of light on plant life is also notable. Every one is familiar with the appearance of grass beneath boards which have been thrown down on a lawn or with the sickly-looking, yellowish sprouts which grow from stored potatoes in spring. Such plants are said to be *etiolated.* Their leaves are usually much reduced, and their internodes are lengthened out. Of course they must eventually die if they do not succeed in reaching the light.

The spectrum of chlorophyll shows a strong absorption band in the red-yellow region and a lesser band in the blue-violet. This means that green light is not utilized in photosynthesis, and, in consequence, the leaf appears green. There is still considerable difference of opinion among students regarding the effect of the various light wave-lengths on plant activities. The consensus of recent views is that red light produces an effect somewhat like that of darkness, while blue light shortens the internodes and leads to stocky growth. The latter effect may be due to the ultra-violet rays.

Only a small amount of the light falling on a leaf is used for photosynthesis. It has been calculated that in bright sunlight 1,200,000 calories of heat energy per square meter of leaf surface are available each hour and that the leaf utilizes only 7/1,200 of this — less than 0.6 per cent. This is sufficient to form between 0.5 and 1 gram of starch. Our best gasoline engines utilize fully 35 per cent of the energy available. Perhaps the apparent inefficiency of the leaf is due to the fact that carbon dioxide is present in too small a quantity to keep the chlorenchyma cells running at full activity. It seems to be true that the plant can utilize more carbon dioxide than is normally present in the air, though an upper limit of availability is soon attained and the plant begins to suffer from physiological disturbances.

As to the actual method by which light energy is transformed into chemical or intramolecular energy in the manufacture of carbohydrates, we have only hypotheses, none well enough substantiated to deserve discussion in an elementary course. In fact, the whole subject of the vegetative physiology of the plant bristles with unsettled problems. The subject is much less advanced than that of the sister science of animal physiology, which has received a stimulus from human medicine. The conclusions derived from much of the older work in plant physiology are vitiated by the failure of the investigators to provide accurate and rigid controls to their experiments.

D. STARCH

Carbon dioxide and water are synthesized into starch in the photosynthetic process. Here again we must confess ignorance regarding the steps involved. A general belief has been prevalent since the time of von Bæyer (1870) that the first compound built up is formaldehyde, yet this substance is very toxic to plants. If it is actually formed in the cells, it must be polymerized immediately to a hexose sugar which in its turn is converted to some disaccharide such as cane-sugar ($C_{12}H_{22}O_{11}$), or to the polysaccharide starch ($(C_6H_{10}O_5)_n$).

More recent investigations of the subject by Moore and Webster (1913–1919) deserve mention. These workers discovered that water and carbon dioxide subjected to light in the presence of colloidal iron are synthesized to a considerable degree into formaldehyde. Now it has long been known that, though chlorophyll contains no iron, it will not form in plants unless iron is present. This led Moore and Webster to a hypothesis that the mass of the chloroplast is composed of colloidal iron and that the chlorophyll is spread in a thin layer over its surface. The function of the chlorophyll, then, according to this view, is merely to polymerize the poisonous formaldehyde formed by the colloidal iron into harmless sugar or starch. It should be realized that all this is pure hypothesis.

Incidentally, it may be mentioned that formaldehyde will appear in quartz tubes filled with water to which carbon dioxide with a trace of alkali is added if the tube is exposed to ultra-violet light.

If we admit the possibility that the synthesis of formaldehyde is the first step in the process of starch formation, then the series of reactions may be empirically represented as follows:

$$CO_2 + H_2O \rightarrow \underset{\text{formaldehyde}}{CH_2O} + O_2$$

$$6CH_2O \rightarrow \underset{\text{hexose}}{C_6H_{12}O_6} \rightarrow \underset{\text{starch}}{C_6H_{10}O_5} + H_2O$$

Starch is the first visible product of photosynthesis and results from the polymerization of sugar molecules with the loss of water. Though we have given its formula as $C_6H_{10}O_5$, it is in reality $(C_6H_{10}O_5)_n$. The value of n is not known. Starch is the commonest of reserve foods in plants. It makes up 50 per cent to 65 per cent of the dry weight of cereal grains and 80 per cent of the dry matter of potatoes. It occurs in the form of tiny granules which are usually of definite shapes, depending on the plant from which they were derived. The starch grains of the potato, for example, are ovoid and vary considerably in size. Under the microscope they show a striking effect like that of a banded agate, since they are made up of many laminæ of starchy substance which are alternately more and less refractive to light. These layers are concentric about a point or *hilum*, which in the case of the potato starch grain is usually slightly excentric. From the hilum small shrinkage cracks usually radiate out into the substance of the grain. The general effect of the potato starch grain is that of a small clam-shell, though it can easily be proved that the grains are not really flattened since they will roll across the field of the microscope without a change in their appearance when the cover-glass is disturbed. Fig. 79 shows bean starch grains in the cells of the cotyledon. Those of *Euphorbia* are shaped like thigh-bones; those of the oat are compound. These forms peculiar to the starch grains of particular plants often make it possible for a trained microscopist to detect starchy adulterants in foods.

The starch grain is really a mass of delicate needle-like crystals which radiate out from the hilum. It is easily hydrolyzed by alkalis or hot water to an amorphous colloidal gel (starch paste). It is stained blue-black by iodine and is the only known organic compound which iodine will stain in this way.

Cellulose is another carbohydrate compound closely allied to starch: in fact, it has the same chemical formula, $(C_6H_{10}O_5)_n$.

E. DEMONSTRATION EXPERIMENTS ON PHOTOSYNTHESIS

Certain experiments to demonstrate the main aspects of photosynthesis are easily performed.

To show that a leaf standing in sunlight contains starch, one need only to detach it and kill with hot water. Hot alcohol will remove the chlorophyll, and a subsequent treatment with potassium iodide solution reveals the bluish-black color imparted to starch.

Now if the plant be placed in darkness for twenty-four hours, the same treatment of a leaf will show that it is wholly free from starch, for the compound has been carried away (translocated) into stems and roots.

If to another living leaf of the same starch-free plant we affix a screen of cork or tin-foil, with perhaps a characteristic pattern cut in it, and then place the plant in bright light for a few hours, starch will be found only in the regions where light can strike the cells. Hence if the leaf be "developed" with iodine, a perfect pattern of the screen will appear in blue-black starch on a yellow ground. Even a photograph can be printed on a leaf from a negative by the same method. The above experiments show, then, that light is necessary to starch formation.

To prove that carbon dioxide is essential to the process, a few green twigs may be placed in a bottle and suspended inside a larger stoppered jar which also contains a beaker of potassium hydroxide solution. A check jar should be set up at the same time without the caustic potash solution. Into each jar a small amount of carbon dioxide should be introduced, since the small volume of air in the jars might contain too little carbon dioxide to give a possitive test. Both jars are exposed to the light. It will be found later that in the jar where the caustic potash solution has absorbed the carbon dioxide the leaves show no starch, whereas in the other leaves it is present.

More definite and quantitative tests of the composition of the gases present before and after such an experiment are not difficult to devise.

88. *Respiration versus Photosynthesis*

All living protoplasm respires all the time. Hence a green plant is constantly giving out carbon dioxide from the cells. As we have seen, however, carbon dioxide is being continually picked up by the photosynthetic activity. Hence during the daytime no carbon dioxide can be detected around the plant. Probably it never escapes from the intercellular spaces but diffuses back into the chlorenchyma.

The fact that the plant has two reverse physiological processes proceeding simultaneously in light, but only one in darkness, has led to several false notions about plants. It is generally believed by laymen that in its gaseous interchange with the air the plant behaves in a manner directly opposite to the animal. We see that this is not true; the plant merely carries on one physiological process that the animal does not, namely, photosynthesis. It is often claimed, too, that plants in sleeping rooms are unhealthful. This belief is based on a hazy idea of respiration. Of course respiration does evolve carbon dioxide, and when light is not available the gas will tend to accumulate around the plant. It may be pointed out that a window full of such plants evolves about as much carbon dioxide each night as would a family of mice living in the room. Furthermore, carbon dioxide is not a poisonous gas; in excess ("choke-damp" of miners) it merely drowns an animal as water does by shutting off the oxygen supply.

89. *Anabolic Activities Following Photosynthesis*

A. TRANSLOCATION

We have seen that starch is drained away from the leaves during the hours of darkness and is carried into stems and roots. This movement of food materials through the plant is called *translocation.* We realize that starch does not dissolve in water; at most it can only pass into the colloidal condition, and colloids cannot undergo osmosis. The question arises then as to the form in which this carbohydrate passes out of the leaves.

If one examines grains of starch from a dry kernel of corn, they will be found to be slightly but smoothly angular. If, on the contrary, starch grains be taken from the region of the endosperm near the cotyledon of a germinating grain of corn, a striking difference is observable. The grains are corroded and possess a roughened and jagged outline; some are even breaking into fragments. At the same time a test will show that sugar has appeared in the kernel.

These facts give us a hint as to what happens to starch in leaves during the night. It is changed into sugar and translocated by osmosis to points of lesser sugar concentration. This movement, as regards its great highway at least, occurs in the sieve cells of the phloëm. It will be recalled that in angiosperms the sieve tubes are protoplasmic cells without nuclei, whose walls, particularly the terminal ones, are beset with perforated areas called sieve plates.

B. ENZYMES

We must now ask how is it possible for starch to turn over so quickly into sugar. The answer must be sought in the activity of those mysterious chemical catalyzers known as enzymes. The word *enzyme* comes from *en* + *zumon* meaning "in yeast." Yeast itself possesses certain powerful enzymes, the best known being *zymase*, which splits sugar into alcohol and carbon dioxide. This typical activity of a specific yeast enzyme has given a name to the whole group of similar organic catalysts.

In the sap of the leaf cells, even as in human saliva or pancreatic juice, is a starch-converting enzyme known as *diastase*. It changes insoluble starch into soluble sugar. It may play a reverse rôle also and turn the sugar back into starch. The latter process occurs in tubers and seeds when the sugar has reached its journey's end and is in excess of the immediate needs of the plant. The activity of diastase is a type of activity which proceeds in bewildering variety in all living bodies. In weak, watery solutions and at relatively low temperatures, chemical reactions proceed with ease under the guidance of enzymes. To bring about the same reactions in the laboratory the chemist must use great heat with strong acids and alkalis. What are these enzymes which do so easily what the best resources of the chemist are strained to accomplish? We do not know. They are certainly non-living chemical substances, but whether mixtures or simple compounds, whether carbohydrate or proteidal, has not been determined. They possess a set of curious properties: they are inactivated by cold and destroyed by heat above 70° C.; they work best in darkness, while bright light weakens and finally destroys them; they can be poisoned and prevented from acting; they cannot be purified, since they adsorb electrolytes with great vigor.

Many of the properties just listed are also characteristic of metals in the colloidal condition. Platinum black, for instance, which is merely colloidal metallic platinum produced by electrolysis, will split hydrogen peroxide like an enzyme; it, too, adsorbs electrolytes with vigor and it can be poisoned by cyanides. Such facts have led some investigators to the opinion that enzymes are colloidal in nature and that their curious properties may depend upon the electrical charges surrounding their particles. The general belief is that they form loose combinations with the substratum and that after effecting atomic reorganizations they themselves split away unchanged.

No enzyme has ever been prepared in a pure state, yet several of economic importance are on the market. The diastase prepared from dried calves' pancreas by elaborate methods of precipitation and filtration can digest 20,000 times its own weight of starch before it is inactivated by the presence of the resultant sugar.

A list of a few prominent plant enzymes will be of interest: *diastase* changes starch into sugar; *cytase* acts on cellulose walls and dissolves them; *invertase* splits cane sugar into fructose and levulose; *lipase* splits fats into glycerin and fatty acid. There are also various *proteolytic enzymes* which split proteins into peptones, amino-acids, etc. In certain molds the following enzymes have been determined: *protease*, *nuclease*, *amidase*, *lipase*, *emulsin*, *amylase*, *inulase*, *raffinase*, *sucrase*, *maltase*, *lactase*, *histozyme*, *catalase*, and *phytase*.

The activity of diastase in converting starch into sugar is associated with an interesting subject which is of considerable importance to the horticulturist who may wish to force certain plants out of season for the winter's trade.

It is known that if one removes certain woody plants in autumn to the greenhouse and attempts to force them into leaf or flower they persistently refuse to grow. On the other hand, if such plants be taken in after freezing weather, they start quickly into activity. Furthermore, it has been discovered that subjection to the fumes of ether or of certain other gases will excite dormant plants into growth. More remarkable still, if the region beneath a leaf bud be vigorously massaged, then that particular bud begins to push out.

The explanation of these curious activities is not far to seek. It will be recalled that in the discussion of the cell it was pointed out that cytoplasm is characterized by a highly vacuolate structure. Now it may be easily understood that starch grains must be kept apart from diastase if they are to be preserved intact. On the other hand, any process which destroys the vacuole membranes will permit the diastase to act upon the starch grains, and as a consequence sugar will appear immediately. Free sugar is necessary to the growth of plants, since starch will not undergo osmosis from cell to cell. Freezing, mechanical massage, or exposure to certain gases breaks down the vacuolar structure of the cytoplasm and releases the diastase, which acts upon the stored starch and converts it into sugar. Then the buds begin to grow.*

In this connection it is of interest to note that cattle may be poisoned by feeding on the wilted leaves of the wild cherry, though the fresh leaves are harmless. The cherry leaf contains a glucoside, amygdalin, and an enzyme, emulsin. When the two compounds are brought together, the amygdalin is hydrolyzed, and one of its derivatives is hydrocyanic (prussic) acid. It is evident that wilting destroys the vacuolar structure of the cytoplasm and brings the glucoside and its hydrolytic enzyme together.

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* F. V. Coville, "The Influence of Cold in Stimulating the Growth of Plants," *Annual Rept. Smithsonian Inst.* 281–291, (1919).

The poisonous nature of peach-pits, cherry-pits, and bitter almonds is due to the same thing. They also contain amygdalin and emulsin in dangerous amounts, and when the cells are crushed by the teeth hydrocyanic acid is formed.

C. THE ENERGY RELATIONS OF ORGANIC COMPOUNDS

We have now finished the introductory consideration of the carbohydrates which are the products of photosynthesis and the basic energy-containing foods from which further compounds are manufactured.

Before passing to the study of these other compounds, however, let us consider a little more closely the energy factor which gives to the carbohydrates their fundamental position in the nutrition of both plants and animals.

As a general rule, we may say that large molecules possess far more internal energy than do small ones; their formation involves an endothermic reaction. We may think of this absorbed energy as converted into static chemical affinity to hold the system of atoms together. But if larger molecules contain more energy, they are also more labile, more likely to go to pieces, and the more energy they contain the greater is their lability.

Plants tend to build up enormous molecules by the summation or polymerization of smaller ones. As an example, we may note that the sugars may form an ascending series from the monosaccharid glucose ($C_6H_{12}O_6$), through the disaccharid sucrose ($C_{12}H_{22}O_{11}$), the trisaccharid raffinose ($C_{18}H_{32}O_{16}$), to the tetrasaccharid stachyose ($C_{24}H_{42}O_{21}$). More commonly, as we have learned, the polymerization leads to starch $(C_6H_{10}O_5)_n$. Under the activity of enzymes these compounds are subsequently broken down to carbon dioxide and water, and the chemical energy which was originally derived from sunlight may be utilized for cellular activities, growth, heat production, or tropismic curvatures.

D. FATS OR HYDROCARBONS

A rearrangement and increase of the atoms of the three elements composing the carbohydrates brings the *fats* into existence. The synthesis of fats takes place largely in leaves and cortex. They represent the energy-containing foods *par excellence*, and are commonly found stored in roots, tubers, or seeds. In fact, many plants have no reserve starch at all, but store their reserves wholly in the form of oil.

Fats are all combinations (esters) of the trihydroxy alcohol glycerin or glycerol with so-called fatty acids. Waxes, which are allied to them, are esters of monohydroxy alcohols. A few common vegetable fats are olive-oil from *Olea europea*, palm-oil from *Elæis guineensis*, cotton-seed oil from *Gossypium*, linseed-oil from *Linum usitatissimum*, and castor-oil from *Ricinus communis*.

E. PROTEINS

Up to this point we have spoken of the utilization of only those chemical elements supplied by water and the carbon dioxide of the air. It is obvious, however, that living protoplasm must be manufactured by the plant and that this necessitates the formation of proteins, the utilization of the salts of nitrogen and often those of sulphur and phosphorus which have been brought up from the soil. Probably, too, certain metallic elements also enter into the formation of the more elaborate proteins.

In spite of the fact that the air consists of about four-fifths nitrogen, the ordinary green plant can make no use of the element in its gaseous form. It must be supplied from the soil and ordinarily in the form of nitrates, though ammonia compounds may remedy a nitrate deficiency to some extent and even organic nitrogenous compounds may be slightly utilized.

The *proteins* are elaborate combinations of amino-acids, these being organic acids with certain hydrogen atoms replaced by the amino group, (NH_2). Their molecules may contain hundreds or even thousands of atoms. Any further consideration would be out of place in an elementary discussion. The subject belongs rather to the great field of plant chemistry.

F. OTHER NON-NITROGENOUS AND NITROGENOUS PLANT COMPOUNDS

The host of other chemical compounds found in the plant can receive but slight mention.

In addition to carbohydrates and hydrocarbons, plants contain two other general groups of non-nitrogenous compounds — the *volatile* or *essential oils* and the *organic acids*. To the former group belong the aromatic substances which give the fragrance to flowers, fruits, and leaves; to the latter belong the acids which give the sour taste to fruits, etc. The commonest of these are malic acid, found for example in the apple, and citric acid, which is characteristic of citrus fruits. The commonest of all plant acids is oxalic acid. It may occur free in the cell sap, though more often it is combined with calcium to form conspicuous crystals. The sour taste of rhubarb is due to a high content of this acid.

In the group of nitrogenous compounds other than proteins may be placed the glucosides, tannins, pigments, and alkaloids.

The *glucosides*, varied and abundant in plants, are combinations of glucose with some other substance — often an aromatic compound. A few examples are salicin from the willow, populin from the poplar, and hesperidin from the orange. It has been pointed out already that members of one special group of glucosides yield hydrocyanic acid when hydrolyzed by enzymes. Of these amygdalin, found in members of the rose family, is characteristic. It is split by the enzyme emulsin and many cases of poisoning have been traced to this source.

The *tannins* are astringent, bitter substances allied to gallic acid ($C_7H_6O_5$).

Pigments include a heterogeneous group of colored compounds. We have already considered chlorophyll in some detail and have mentioned xanthophyll and carotin. The blue and red anthocyanins are glucosides.

The *alkaloids* are nitrogenous compounds related to pyridine. Many are extremely poisonous. A few of those better known are coniine from *Conium maculatum*, the "poison hemlock" by which Socrates was put to death; nicotine from tobacco; atropine from the nightshade (*Atropa Belladonna*); strychnine from *Strychnos Nux-vomica;* quinine from species of *Cinchona;* and morphine from the opium poppy.

The rôle of most of the above compounds in the physiology of the plant is very obscure. To consider but a single group, the alkaloids, some botanists hold that they are essential to the well-being of the plant; others believe that they are waste products resulting from proteidal decomposition and that their rôle is analogous to that of urea in the animal; it has been suggested by still others that their noxious taste exercises a protective function by keeping away herbivorous animals.

90. *Conclusion*

As a conclusion to this chapter a comparison of the vegetative system of the plant to a great transporting and manufacturing system may be apt.

The cauline xylem with its extension into the leaf-traces and veins is like a pipe-line along which raw materials — water and salts — are transported to a factory (the leaf). Through its doors (stomata) the factory receives its other necessary raw material (CO_2). In the laboratories (chlorenchyma cells) the sun-engines (chloroplasts) start up, and finally the laboratory product (starch) begins to appear.

As the source of power is withdrawn at night, the manufactured product is converted into sugar, dissolved in water, and moved through another pipe-line (phloëm) to various storage warehouses (parenchyma of stems or roots). Some of it may be utilized at once to increase the size of the "plant" or to supply energy for work or for the further synthesis of other compounds.

The slight sketch of vegetative physiology given in this chapter will perhaps open the door to the extreme complexity of the subject and show the crying need for trained and competent investigators.

CHAPTER XV

THE REPRODUCTION OF SEED PLANTS

91. *Introduction*

In this, the last chapter of Part II, we find ourselves completing the circle of our studies and coming back to the subject of the seed and its origin.

We are already familiar with the macroscopic aspect of the flower, and we know that it is the part of the plant which is concerned with seed formation. We realize, too, that the transference of pollen from anthers to stigmas is usually a necessary antecedent to seed formation, and that wind, water, and insects are impressed into the service of the plant to carry the precious pollen grains.

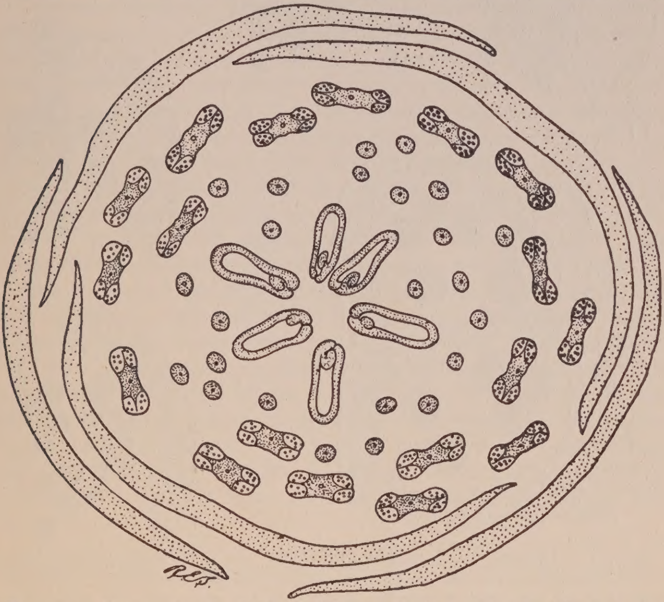

FIG. 141. — Cross-section of a *Caltha* Bud Showing Sections of the Floral Parts (x10).

In Fig. 141 is represented a cross-section of the *Caltha* flower with

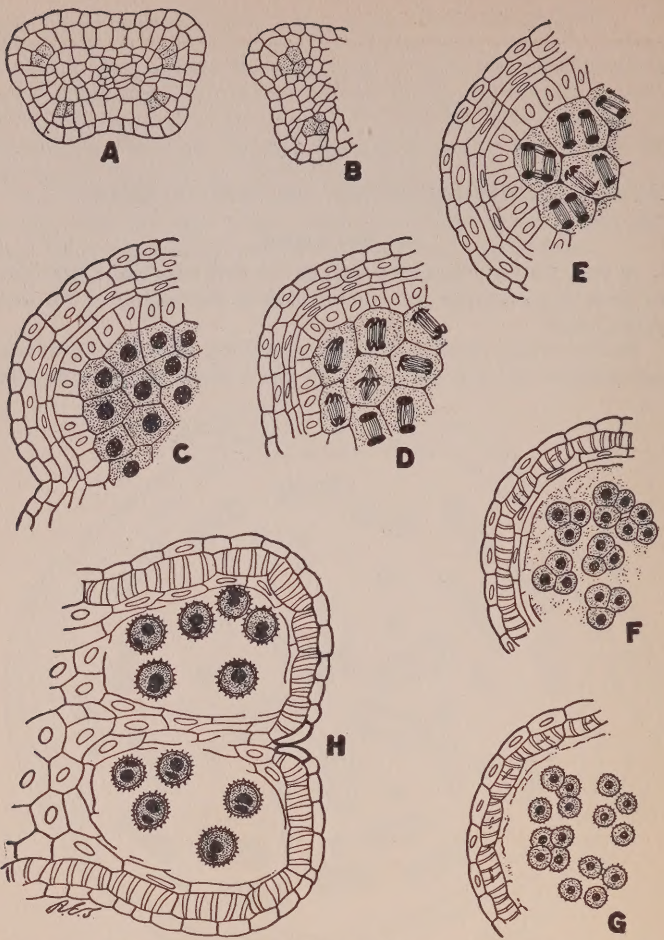

FIG. 142. — Microsporogenesis in an Angiosperm: A, very young anther in cross-section showing the four groups of cells (archesporium) whose multiplication produces the sporogenous tissue; B, stage slightly later than A; C, portion of young anther in cross-section showing spore mother cells (microsporocytes); D, spore mother cells undergoing heterotypic mitosis (meiosis). At this point the chromosomes are reduced from *2n* to *n;* E, second or homotypic mitosis which brings four nuclei into existence in each mother cell, each possessed of *n* chromosomes; F, organization of microspores into tetrads, one of which in each case lies behind its three fellows; G, break-up of the tetrads into free pollen grains (microspores); H, pollen grains lying free inside the mature locelli (microsporangia) of the anther. It should be observed that a special jacket of large cells (tapetum) surrounds the spore mother cells; it breaks down in stage F and serves to nourish the developing spores. The striations on the layer of wall cells beneath the epidermis in F, G, H constitutes an elastic dehiscence mechanism for opening the anther-sacs along the stomium.

all its parts in place. Around the outside lie the imbricated sepals; next come the sectioned anthers with pollen grains in the locelli. The small circles which follow are sections of stamen filaments, and the center of the figure is occupied by six carpels with ovules inside them.

92. *The Genesis of the Pollen Grains*

If a very young anther be cut in cross-section, it will be discovered that inside the protective wall lies a set of angular cells which possess large nuclei imbedded in densely granular cytoplasm (Fig. 142, C). These are the *pollen mother cells* and each of them is destined to produce four pollen grains. The genesis of the pollen grains involves a rather complex modification of the chromosome conditions of the nuclei.

Let us suppose for a moment that each pollen mother cell has been converted directly into a pollen grain and let us assume that its nucleus carries six chromosomes. When this nucleus or its derivative, united with another nucleus in the ovule (which is the essential fact of fertilization) the result would be a cell whose nucleus contained twelve chromosomes. This cell would produce the embryo, and in consequence the next generation would carry twelve chromosomes in all its cells. When it in turn came to form its pollen grains, they would contain twelve chromosomes instead of six, and as each united with another cell, the number would swell to twenty-four. Something, then, must be done to prevent this progressive accumulation of chromosomes.

Let us remove one of the pollen mother cells of Fig. 142, C to a new figure (Fig. 143) and follow its subsequent development. At A is shown the large nucleus with its six chromosomes. At B it is evident that the chromosomes are uniting in three pairs. It is known that the units which pair in this fashion are derived respectively from the maternal and paternal plants of the previous generation. It is known, furthermore, that in this stage the two masses of germ-plasm interchange or mix together their various hereditary factors (*genes* or *determinants*) so that when they separate again they have been modified qualitatively.

The chromosomes now orient themselves at the equator of the cell and develop the familiar mitotic spindle (Fig. 143, C). Thereafter they are slowly pulled apart, so that three of them are drawn to the north pole and three to the south pole (Fig. 143, D). Finally a nuclear membrane is regenerated around each set of three chromosomes, a wall forms at the equator, and two new cells have come into being whose nuclei carry but one-half the number of chromosomes possessed by the parent cell. This constitutes the phenomenon of *chromosome reduction* or *meiosis* or *heterotypic mitosis*. It is immediately followed by a normal mitotic division of each cell, so that four cells, each carrying a nucleus possessing three chromosomes, finally arise inside the pollen mother cell. These four cells constitute a tetrad of pollen grains. Each one develops a double wall around itself. The outer, called the *exine*, is usually cutinized and often bears tubercles or spines or net-like markings. Certain shapes of pollen grains and certain types of sculpturings are characteristic of particular plant families. The inner coat, called the *intine*, is composed of cellulose and is of a thinner and more delicate nature.

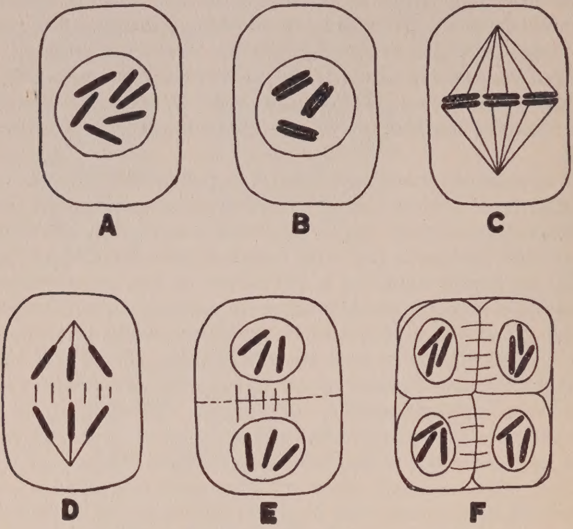

FIG. 143.—Diagrammatic Representation of Microsporogenesis and Accompanying Chromosome Reduction (Meiosis). The diploid chromosome number is represented as six, the haploid as three. A, the six chromosomes are distributed through the nucleus of the pollen mother cell (microsporocyte); B, the chromosomes are in synapsis (three synaptic pairs); C, the metaphase state; D, separation of complete chromosomes in the anaphase; E, telophase; chromosome reduction from six to three accomplished; F, a second normal mitosis in each cell has brought four pollen grains into existence, each with three chromosomes.

In the preceding treatment we have used six and three as arbitrary chromosome numbers. The terms which do duty for all similar numerical changes are *diploid* (*diploos* = "double") and *haploid* (*haploos* = "single" or "simple"). Or, if we wish to use a symbol to designate the two conditions, they may be called $2n$ and n. The reduction of the chromosomes from $2n$ to n is assurance that the succeeding generation shall bear the chromosome number ($2n$) of its parent.

Meiosis occurs in animals as well as in plants, so that both the sperm cells and the egg cells are formed in tetrads likewise, though three of the eggs of each tetrad fail to mature.

If we return now to Fig. 142, we shall better understand the succeeding stages. In D, meiosis is taking place; in E, the subsequent normal division of the nuclei (homotypic mitosis) is in progress; in F, the tetrads of pollen grains have appeared (the fourth member may be supposed to lie behind its three brothers in each case). In G, the tetrads have developed a prickly exine, and they are falling apart to form the familiar powdery mass of pollen grains. In H appear two mature locelli on a larger scale, with a few pollen grains inside them. The wall cells which form the partition separating the two locelli generally break down so that the two cavities merge into a single one, which is known as the *anther-sac* or *anther loculus*. Fig. 142, H, shows us also that just underneath the epidermis is a layer of wall cells covered with cross bands. It constitutes a *dehiscence mechanism*. As the cells dry out, the layer serves to open the anther-sac lengthwise along a median line called the *stomium*. Two of the thick-walled stomial cells are shown in cross-section in our figure. The dehiscence layer was derived in evolution from an extension of the fibro-vascular bundle of the stamen filament.

93. *The Development of the Ovule*

The primordium of the young ovule is an ovoid cellular mass which is known as the *nucellus*. The two *integuments* which eventually form the testa and tegmen of the seed arise at an early stage at the base of the nucellus and proceed to roll slowly over it somewhat as the acorn-cup might be rolled over the acorn (Fig. 144). The inrolled margins of the integuments do not, however, completely meet, and a small pore, known as the *micropyle*, is left open at the free end. Their place of origin at the base of the nucellus is called the *chalaza*. The funicle is attached to the same region.

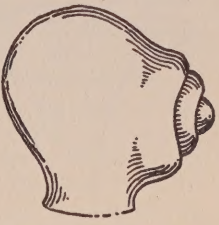

FIG. 144.—Anatropous Ovule Partly Developed.

It would be of small moment at this time to consider very closely the complicated activities which proceed inside the nucellus in preparation for the formation of the embryo. Such a consideration may better be delayed till we come to the reproduction of the angiosperms in the closing pages of Part III.

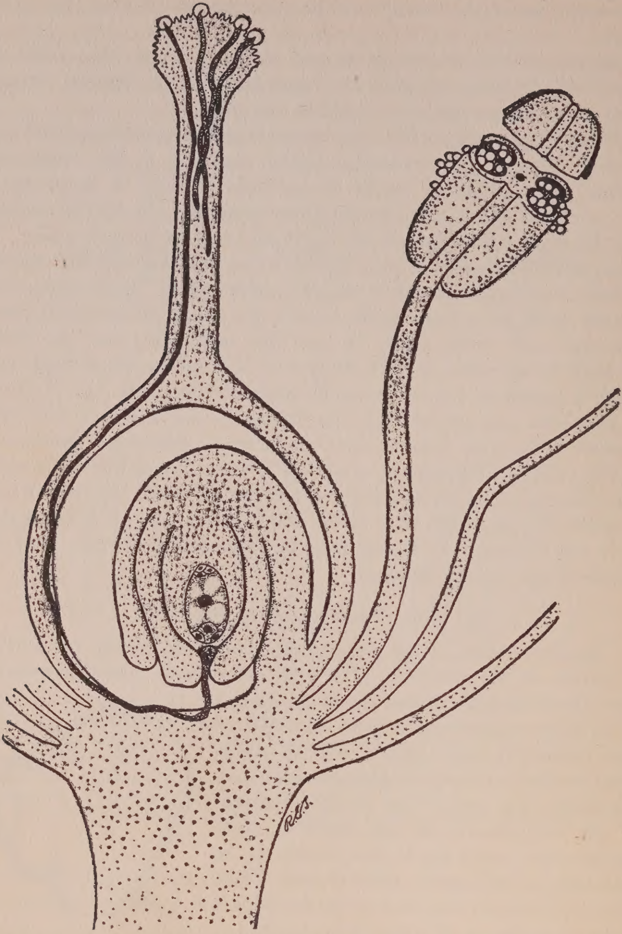

Fig. 145.—Structure of the Reproductive Parts of an Angiosperm at the Time of Fertilization. Pollen grains are being shed from the anther, which is represented as cut in cross-section. Pollination has already occurred, and the pollen grains have germinated and are sending their tubes down into the style. Since there is but one ovule, only one pollen tube functions; it has already penetrated the micropyle and is about to discharge its two sperm-cells.

It is sufficient to say here that a process of chromosome reduction takes place in a single mother cell inside the nucellus and that this leads eventually to the formation of a large cell called the *embryo-sac*, within which, in the majority of cases, a group of eight cells develops. One of these eight cells is an egg which, after fertilization by a sperm derived from the pollen grain, is capable of developing into an embryo plant.

94. *Pollen Tube Development*

While the ovule is maturing, the pollen grain has reached the stigma of the carpel. As it lies there it begins to swell by absorbing liquid from the moist secretion. Turgor pressure bursts its exine, the intine protrudes through the cleft and proceeds to grown downward through the loose parenchymatous tissue of the style. It has now become the *pollen tube* (Fig. 145). Sometimes it forces the obstructing cells apart; sometimes it dissolves them by enzymatic action.

Meanwhile the haploid nucleus of the pollen grain has divided by mitosis to form a *tube nucleus*, which presides over the activities of the pollen tube, and a *generative nucleus*. The latter divides again, and two *sperm nuclei* are brought into being. They are rather elongated curved bodies and exhibit a slight amœboid movement. As the tube pushes forward, its protoplasm pulsates actively. Finally, in a period varying from six hours to six months in different plants, it reaches the ovarial chamber and swings forward to the micropyle of an ovule by the shortest convenient route. It pierces and destroys the nucellar tissue in its path and presses into the embryo-sac. Then its tip bursts open and the two sperm cells are discharged into the cavity.

95. *Double Fertilization*

One of the sperm nuclei unites promptly with the egg nucleus. This constitutes the act of *fertilization* or *zygosis*. Since both the egg and the sperm are in the haploid condition, fertilization now restores the diploid state, which is perpetuated in the embryo that shortly arises from the fertilized egg. The second male nucleus does not perish. It also effects the fertilization of a nucleus inside the embryo-sac which is later concerned with the formation of the endosperm, that fleshy nutritive tissue which we saw in the seed of the castor-bean. Since both sperm nuclei unite with nuclei inside the embryo-sac, the process is known as *double fertilization.* It is represented diagrammatically in Fig. 146, A.

96. *Embryology and Endosperm Formation*

The fertilized egg or zygote now develops into the embryo by successive cleavages accompanied by rapid mitoses. It slowly forms

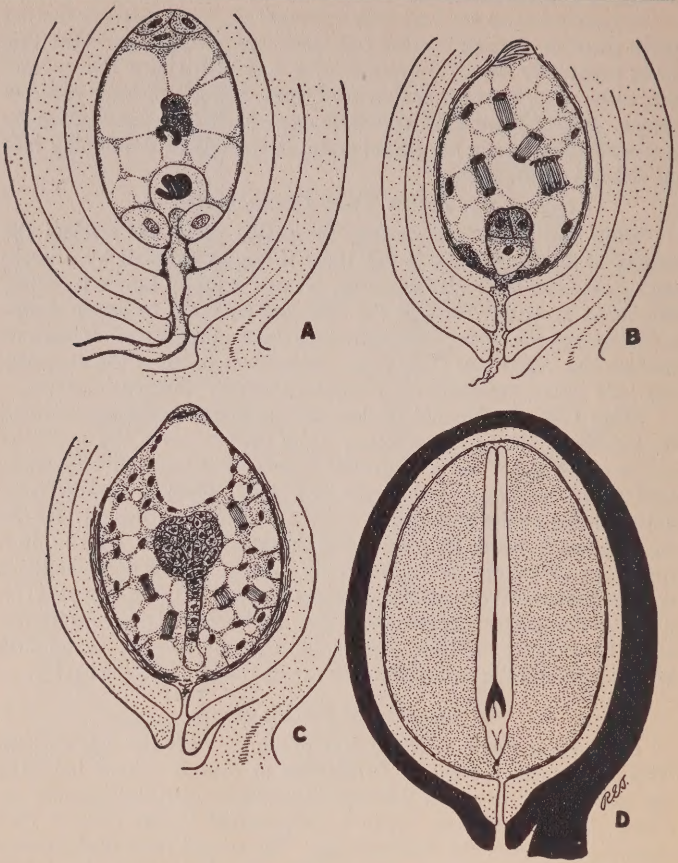

FIG. 146. — Fertilization or Zygosis in an Angiosperm and the Subsequent Embryology: A, the pollen tube has burst and expelled the two sperm, shown as black coiled bodies. One of these is uniting with the egg, converting it into the zygote, and the other with the primary endosperm nucleus, converting it into the definitive endosperm nucleus; B, early embryology and endosperm formation. The egg has divided to form a three-celled embryo; the endosperm nuclei have undergone several mitoses. C, later stage in embryo and endosperm formation. The embryo has differentiated a filamentous suspensor which thrusts it deeper into the endosperm. Cleavage walls are cutting into the endosperm. The nucellus (represented by wavy lines) is being crushed by the growth of the endosperm; D, mature seed of a dicotyledonous angiosperm. Testa represented in black, tegmen lightly stippled, endosperm more heavily stippled, embryo in white. The nucellus has been crushed to a mere membrane inside the tegmen.

a mass of meristematic tissue which differentiates into cotyledons, plumule, and hypocotyl. The endosperm nucleus, too, begins rapid division and fills the embryo-sac around the embryo with myriads of nuclei (Fig. 146, B, C). Finally the nuclei and accompanying cytoplasm are organized into the richly nutritive tissue called endosperm (Fig. 146, D); its cells become gorged with starch, oil, or proteid which enters in soluble form through the fibro-vascular strand which runs through the funicle. The nucellar tissue is usually crushed out of existence by the expanding embryo and endosperm so that it becomes a mere membrane of collapsed cells. If the seed is of the exendospermous type, during its ripening the cotyledons actively digest and absorb the surrounding endosperm and become the bulky organs so familiar to us in the bean and pea. This, as we learned in Chapter I, inhibits their foliar activity so that they finally cease appearing above ground at all and the seed is characterized by hypogean germination.

So our studies have led us back to the beginning of this book; the ovule has been transformed into a seed with testa and tegmen surrounding an embryo, either with or without endosperm, and the plant is prepared to enter upon a new cycle of its life.

97. *Conclusion*

Part II of this book has doubtless opened up a new world to us. We have struggled with unfamiliar facts and a difficult terminology. From time to time we have stood at the very fringe of scientific research where the technique of exploration is so difficult that the various workers disagree vigorously over results. Perhaps we had expected that the microscope would solve some of the mysteries of the world; yet, probing the cell itself, we found ourselves no closer to Life. The study of chromosomes and mitosis did not clear up the mystery of the creation of the plant. If we turn back again to the quotation which stands at the Introduction to Part II we read " — a mystery which no machinery can probe."

Yet there are many problems whose proximate solutions lie within the limited domain of science. The student must have wondered about the origin of the seed plants. Where did they come from? What kinds of plants preceded them in the earth's history? What is the meaning of those reproductive details with which we have just been struggling, the terminology of which we have tried to learn by a sort of mental *tour de force*, trusting that we might understand it later?

It is to answer such questions as these that we turn now to Part III.

PART III

THE EVOLUTION OF THE PLANT KINGDOM

INTRODUCTION

In the coming pages of this book we are to study the chain of life which stretches from the bacteria to the seed plants. Out of the darkness which surrounds the beginnings of life we shall emerge into a twilight zone of archaic and peculiar water plants which are quite foreign in their structure to the dominant green vegetation of the earth with which Parts I and II have made us familiar. As the study proceeds we shall discover remarkable experiments in architecture, odd adaptations to the aquatic habitat, exquisite forms and geometrical designs which, perhaps, express the workings of a mathematical intelligence behind Nature — that same intelligence which relegates the atoms and molecules to fixed mathematical positions in crystals. We shall follow briefly the story of the transmigration to the land and witness its culmination in the group of splendid seed plants.

The treatment of the subject, so far as the limited compass permits, will be an evolutionary one. Without that quickening spirit the facts of plant structure and function would remain forever a heap of dry bones.

A. THE BROAD CLASSIFICATION OF THE PLANT KINGDOM

At the outset let us examine a broad outline of the classification of plants which we shall follow, though it is not my intention to devote very much time to this technical aspect of botany in the coming elementary studies.

There is no generally accepted system of major divisions of the plant kingdom, and the one set down here attempts to embody the good points of several systems. It is one which appeals particularly to a botanist who tries to look at the plant world from the standpoint of evolution.

The plant kingdom may be divided into two great sub-kingdoms which are known respectively as *Thallophyta* and *Embryophyta*. The former is an utterly unnatural grouping of plants whose members have no true stems, roots, or leaves. It embraces such diverse forms as minute, unicellular bacteria, and giant seaweeds over 200 feet long. It constitutes a convenient artificial category in which to place the remnants of many lowly and archaic lines of evolution.

Setting aside the well-defined class of *Schizophyta*, which includes the bacteria and the blue-green algæ, the remaining members of the *Thallophyta* may be distributed among the *Algæ* and the *Fungi*. The algæ bear chlorophyll and are autotrophic; the fungi, on the contrary, possess no chlorophyll and are forced to assume a saprophytic or a parasitic life.

The algæ, in their turn, are divided upon a basis of color into three evolutionary series: the chlorophyte line, the phæophyte line, and the rhodophyte line, which, in a broad sense, means green plants, brown plants, and red plants. These terms have no true classificatory value, but they serve to divide the algæ into convenient groups for study. Within these groups we shall recognize such classes, orders, families, genera, and species as occasion demands.

The members of the *Embryophyta* stand opposed to the *Thallophyta* as a natural alliance of plants whose common ancestors left the water long ago. All of them possess an organ — the archegonium — in which the young embryo is given a start in life. The natural division of the *Embryophyta* is into the *Atracheata*, or mosses, and the *Tracheata*, which includes all other higher plants, such as club-mosses, horsetails, ferns, and seed plants. The *Atracheata* have no tracheids in their stems; the *Tracheata*, on the contrary, possess these water-conducting elements.

In summary, then, the scheme of classification adopted in this book runs as follows:

Kingdom *Plantæ*

- Sub-kingdom *Thallophyta*
  - Division I. *Schizophyta* (bacteria and blue-green algæ)
  - Division II. *Algæ* (*Phycophyta*)
    - a. Chlorophyte Line of Green Algal Plants
    - b. Phæophyte Line of Brown Algal Plants
    - c. Rhodophyte Line of Red Algal Plants
  - Division III. *Fungi* (*Mycophyta*)
- Sub-kingdom *Embryophyta* (*Archegoniatæ*)
  - Division I. *Atracheata* (*Bryophyta*)
  - Division II. *Tracheata*

B. THE ORIGIN OF PLANTS

Any attempt to tell the story of the evolution of plants forces the botanist at the very outset into the twilight of speculation which surrounds the beginnings of life on earth. How did it all start, anyhow? Well, science is not concerned with metaphysical ultimates, though an inquiry into the proximate origin of living things is a perfectly legitimate scientific question. As was pointed out in Part II, most biologists hold to some form of the theory of spontaneous generation of protoplasm out of inorganic matter. We may suppose that if the scientist could have stood upon the shores of the pre-Paleozoic sea and if his life span could have been extended long enough, he would have witnessed the slow transformation of inorganic matter into protoplasm and eventually into organisms of progressive complexity. The faint stirrings in colloid and crystal and the simulacra of adaptive tropisms which are visible in inorganic matter suggest that life, "cribbed, cabined and confined," is striving against the grip of all but inflexible mechanical law. As Leduc has said, the transition from such systems of inanimate colloids to living things is "gradual and insensible."

It is still too early to say what is to be the final resolution of the problem of the filtrable viruses — those particles invisible to the microscope which cause certain diseases and which are so tiny that they can pass through porcelain filters. In view of the widespread hierarchical principle which prevails in Nature, the writer would not be surprised to learn that the cells of the bacteria arose from the compounding of such particles, and that the bacteria, in their turn, were aggregated into the nucleated cells of the higher plants and animals, even as Minchin and Wallin, among others, have suspected. We need not linger in this realm of speculation any longer, but may advance at once to the consideration of the lowest forms of plant life.

CHAPTER XVI

SCHIZOPHYTA (BACTERIA AND BLUE-GREEN ALGÆ)

At the very base of the evolutionary tree stands a group of extremely simple forms of plants which are known as schizophytes, and whose two minor groups are commonly called the bacteria and the blue-green algæ, respectively. The name *schizophyte* means "splitting plant" or "fission plant" and has reference to the only method by which these plants are known to increase, namely, by the splitting of one cell into two. Most plants have some sort of specialized reproductive cells, but the schizophytes seem to be without such.

They include the smallest of all plants, and their cytological equipment bears the stamp of a great antiquity. In discussing the structure of the cell in Part II we have already had occasion to note that 1,000,000,000 micrococcus cells could easily swim around in a cubic millimeter of water. The schizophytes possess no nucleus, and the chlorophyll-bearing members seem to have no chloroplast. Many of them exhibit remarkable ecological relations to the chemical, physical, and biotic factors of the environment. Last of all they represent the earliest known fossils and have been found in pre-Paleozoic rocks.

I. The Bacteria (Schizomycetes)

It is difficult to give any adequate treatment to this class of plants in a brief work such as the present. Because of their remarkable economic importance the bacteria have been studied much more extensively than have plant groups far higher in the scale of life, and a special science of bacteriology has developed with its own elaborate technique for their investigation.

98. *Distribution*

The bacteria are ubiquitous in nature and occur in such prodigious swarms of individuals that the imagination is staggered by the figures. In soil and water, in dust driven about by the wind, on the skins and in the digestive canals of animals, flourishing in the secretions produced by plants, swarming in all decaying and fermenting organic matter, in pools of snow-water and in hot springs, these tiny beings carry on their lives. Several millions inhabit a gram of ordinary field soil, while in the excrement of animals they may rise to the prodigious number of eighteen thousand million per gram.

As a point of departure for more detailed study we might begin our consideration of bacteria by examining the water from a dish in which beans are decaying. It appears turbid and has an odor which beggars description. A drop of it placed on a slide and studied with the highest power of the microscope will reveal myriads of minute rods and dots, some motionless, some oscillating and tumbling about; some floating singly, others hanging together in chains or aggregated into masses.

99. *The Bacterial Culture*

For careful, detailed knowledge of these small beings it will be necessary to call to our help the special technique of the bacteriologist. We shall find that he has devised methods for isolating the various species and for growing them in pure cultures. The modern and almost universal method of procedure is to employ hardened nutrient agar or gelatin as a substratum upon which each type builds up its own specific colony, characterized by definite form, margin, and color, as well as liquefying and fermentive powers. The colors of such colonies are usually whitish or grayish, but yellow, orange, pink, red, blue, and purple are all known. *Bacterium fluorescens*, for example, imparts a greenish phosphorescence to the medium in which it grows; *Bacterium cyanogenes* stains milk a sky-blue color, while the remarkable *Bacterium prodigiosum* deserves mention because of its vivid history. Its colonies are bright red in color and appear like spots of blood upon bread, meat, and other foods. In the Middle Ages it often appeared during warm, damp weather upon the consecrated Host and was a wonder to the people, who witnessed the miracle of "wounds upon the body of our Lord."

100. *Shapes and Sizes*

The shape of the individual bacterial cell varies considerably, ranging from globose or ellipsoidal to cylindric (Fig. 147). The globose cell is called a *coccus* (pl. *cocci*); the rod-shaped one is a *bacterium* or, when ciliated, a *bacillus*. Sometimes it is twisted or even thrown into spiral coils and it is then called a *microspira* or a *spirillum*. When such contorted cells are dried upon glass, they take the form of a comma or an undulating line. Bacteria vary in size from the remarkable *Hillhousia mirabilis*, which lives on wet mud and whose cells are one-tenth millimeter in length, to the micrococci, which measure but 0.1 to 0.2 microns in diameter. Sometimes the cells live free, but very commonly they build up irregular clusters (*staphylococci*), chains (*streptococci*), or even cubical masses (*Sarcina*) which arise through a very regular division in three planes of space.

101. *Cytology*

The resolution of the cytology of the bacteria offers great difficulty because of the small size of the cell. There is, however, a cell wall made of "bacterial cellulose," and this is usually surrounded by slime in such copious amounts that the aggregate bacterial cluster appears to the naked eye like a mass of jelly. Such is the true nature of "mother of vinegar," formed by *Bacillus aceti*. The investiture of slime may be quite dense. Then it constitutes a *capsule*, or, when it clothes a filament, a *sheath*. *Bacterium vermiforme* (Fig. 148) can shove itself forward over a substratum by secreting abundant slime from one end of its body. Sometimes a single cell of this species may divide, in which case the several daughter cells build up long, radiating slime projections as they are moved outward.

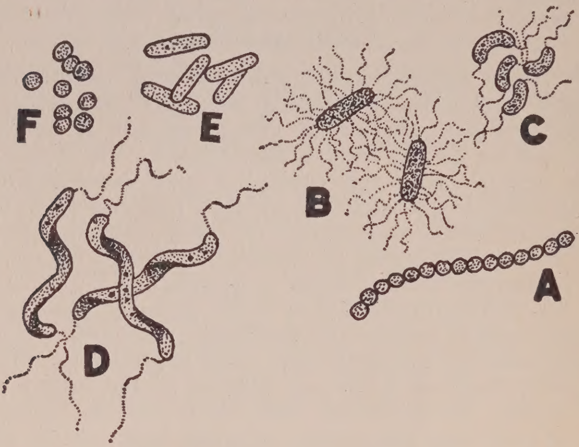

FIG. 147. — Common Forms of Bacteria: A, streptococcus; B, bacillus; C, microspira; D, spirillum; E, bacterium; F, micrococcus.

The protoplasm of the bacterial cell is usually very dense. Granules can often be detected, but there is no nucleus, although grains of chromatin-like material can be brought out by appropriate stains. The cells of the sulphur bacteria are often loaded with amorphous sulphur granules.

102. *Motility*

Many bacteria are motile; they usually travel about 1 to 1 1/2 times their own length per second, though there are certain record-breakers which attain a speed five to ten times as great. This motion is due to *cilia* of varying numbers and of various distribution over the cell, as indicated in Fig. 147.

103. *Reproduction*

Bacteria cells increase by division or fission, which under favorable conditions leads to extremely rapid multiplication. The cells may divide every half-hour, and if one delights in the mathematics of geometrical progression, it may be calculated that after eight hours a single bacterium might have a progeny of about 60,000 descendants. It has been computed that in one and a half days the product of a single bacterium might weigh some 10,000 tons. As an actual fact, the struggle for existence is far more intense among the members of the earth's microflora than it is among her macroscopic plants. They are poisoned by the products of their own metabolism; or one species may inhibit the activities of another by its chemical secretions, or by changing the hydrogen-ion content of the medium where they grow. Protozoa in vast numbers prey upon bacteria. When bacteria invade the animal body, swarms of leucocytes come rushing to the infected area to devour them, while the body cells provide special secretions to dissolve and destroy them.

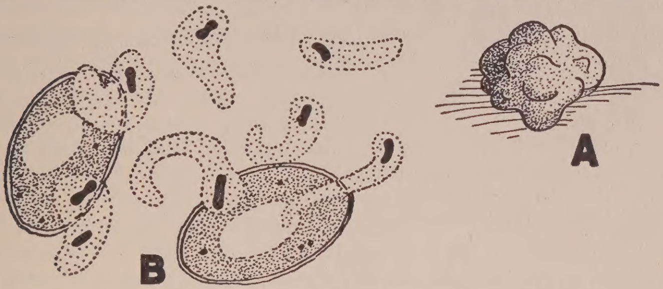

FIG. 148. — Ginger-Beer "Seed" — a Symbiotic Association of *Bacillus vermiforme* and the Yeast *Saccharomyces pyriforme:* A, habit sketch of the dried "seed"; B, slime-invested *Bacillus* with yeast cells.

104. *Spore Formation*

The bacterial spore arises inside the cell and in consequence is called an *endospore* (Fig. 149, A). In the process of its formation the protoplasm contracts from the wall, surrounds itself with a thick membrane, and becomes highly refractive to light. It does not serve for reproduction but is a means of tiding the plant over unfavorable conditions. Such endospores have an amazing power of resistance to influences which would kill any other form of plant life in short order. They will sometimes stand live steam for fifteen to twenty hours. A case is on record where the spores of *Bacillus mesentericus* survived the application of dry air at a temperature of 310–320° C. for thirty minutes, live steam for twenty-four hours, and boiling 4 per cent hydrochloric acid for half an hour.

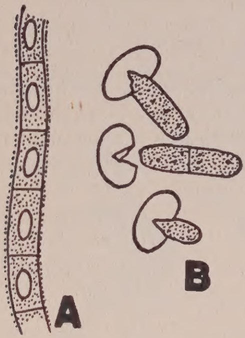

FIG. 149. — Bacterial Spores: A, chain of bacterial cells containing endospores; B, germination of spores.

105. *The Metabolism of Bacteria*

Bacteria are the great destroyers and transformers. Since they are devoid of chlorophyll, they cannot usually synthesize carbohydrates, and in consequence they are forced to turn elsewhere than to direct sunlight for their energy supply. Hence they become saprophytes and parasites, breaking down and destroying organic matter through the activity of enzymes which they secrete. The result of their physiological activities is an elaborate chemistry of metabolism, much of which is included under the terms *fermentation* and *putrefaction*. Some bacteria require free oxygen for their activities; others can extract it from organic compounds and can live in an oxygen-free medium. Hence they can grow under water or inside the bodies of plants and animals.

A. RELATIONS TO NITROGEN

The relations of bacteria to nitrogen are varied and peculiar. They may be comprehended under the terms *denitrification* and *nitrogen fixation*. The former process leads to the loss of nitrogen from organic compounds and is usually associated with the work of anærobic bacteria. Nitrogen fixation, on the other hand, is a reverse process whereby bacteria absorb free nitrogen from the atmosphere and synthesize it into proteidal compounds directly. The soil organism *Azotobacter* is best known for this activity, though many other nitrogen-fixing forms are recognized.

A few words should be said in regard to *Bacillus radicicola*, the organism which forms the well-known root-nodules of various leguminous plants. These excrescences are really malformed adventitious rootlets stimulated to develop through the excitation caused by invading bacteria which enter the root-hairs and proliferate inside the cells of the cortex. Much discussion still revolves around the whole question of the assumed symbiotic relation of the bacteria and the legume, and the method of fixation and transference of nitrogen to the host plant.

B. RELATIONS TO CARBON-CONTAINING GASES

The relation of certain bacteria to carbon-containing gases is no less remarkable than the relation to nitrogen. It has been discovered that many nitrifying, oxidizing, "sulphur," and "iron" bacteria can utilize free atmospheric carbon dioxide, or even methane or carbon monoxide, and can synthesize carbohydrates therefrom. These facts are of the highest evolutionary significance.

C. HEAT PRODUCTION

A marked rise in temperature is associated with the activities of many bacteria. It is, of course, upon this phenomenon that the efficacy of the hot-bed depends as an agency for forcing plants out of season. The peculiar phenomenon of spontaneous combustion is also attributable to certain bacteria which may raise the temperature of hay or old rags to such a point that the mass takes fire. The ignition is usually very sudden and is comparable to an explosion. This has led to the opinion that certain inflammable gases, such as hydrogen or methane, produced by the bacteria themselves, are the immediate agents concerned.

106. *The Economic Importance of Bacteria*

It is impossible to give here any but the most cursory treatment to the vast subject of the economic importance of bacteria. They play a prominent part in the dairy industry, since they transform milk-sugar into lactic acid; split fats into glycerol and fatty acids, thereby imparting rancid flavors to butter; break down proteids into peptones and amino-acids; and lend various flavors, desirable or undesirable, to milk products. In relation to the fertility of soils their rôle is marked. They can decompose cellulose products into "humus," set ammonia free, change nitrites into nitrates, etc. Like yeasts they can transform sugars into alcohols, and alcohols into acetic acid. In connection with the fermentation of sugars we may mention that peculiar substance known as "ginger-beer seed" (Fig. 148). In its dry state it is a granular or lumpy yellowish material. When added to liquids containing sugar it starts a rapid fermentation into "beer." It is composed of the anærobic *Bacterium vermiforme*, already mentioned, and the yeast *Saccharomyces pyriforme*, living in symbiotic association. "Seed" of similar nature has been used by primitive people from time immemorial for fermenting milk.

II. THE BLUE-GREEN ALGAE (SCHIZOPHYCEÆ)

The blue-green algæ are closely allied to the bacteria. They inhabit ponds and ditches, or may even be found abundantly on moist soil, rocks, or tree-trunks.

107. *Field Collecting*

Perhaps the best way to start our study of them is to provide ourselves with a set of small bottles and a small skimming net made of closely woven cloth, and adventure forth into a region of swamps and ponds, not neglecting any ditches or watering troughs along the way, and keeping our eyes open for slimy bluish-green or bottle-green growths floating on the water surfaces, adhering in gelatinous coats to submerged sticks and stones, or even to trees and wet soil, or streaming out in tufts in running water. They often grow much intermingled with the green algæ but the color and a characteristic penetrating "swampy odor," or, as some describe it, "an odor of moldy hay," allows one to discriminate them. The skimming net passed through the water or used as a filter will sometimes enable one to collect minute floating forms which would otherwise be overlooked. So far as possible we will keep the various forms separate in bottles and return with them to the laboratory and to the compound microscope. If we wish to preserve them for later study, they will mostly live for months in battery jars containing plenty of pond water.

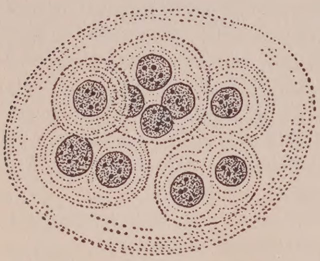

FIG. 150. — *Glœocapsa.* Single colony showing gelatinous coats.

108. *Representative Genera*

A. GLŒOCAPSA — A UNICELLULAR SPECIES

In such collections we are likely to discover *Glœocapsa* (Fig. 150). It is a minute form which sometimes builds up thin irregular layers of bluish-green jelly which adhere to sticks and stones. If a bit of the jelly be crushed under a cover-glass, it can be seen to be composed of myriads of minute globose cells which are bluish-green in color and surrounded individually by laminated coats of jelly, which is a secretion from the cells themselves. The individuals show little cytological detail beyond a few scattered granules which are known to be reserve carbohydrate food. Some may perhaps be seen in process of division. As in all the schizophytes, this is the only method of reproduction. A ring of cellulose grows in from the periphery of the cell and cuts it into two parts. Then each portion proceeds to secrete an independent coat of jelly. Thus it comes about that two or more cells will sometimes be invested by a common capsule — the outer one being secreted originally by the parent cell.

B. OSCILLATORIA — A FILAMENTOUS REPRESENTATIVE

This is a common plant found both floating and attached. In curtain-like masses and strings it often persists indefinitely in culture-jars in a laboratory. It runs into numerous species set apart on size of filaments, shape of cells, sheath characters, etc. This plant has a remarkable property in that its threads can creep from place to place. If one places a tuft of *Oscillatoria* in a watch-glass of water, one observes in a few hours that the filaments radiate outward in a bluish-green film closely applied to the bottom of the glass. Under the microscope the threads can be seen to keep up a curious oscillating and sliding motion. The mechanism of this movement is unknown, though many believe that delicate pseudopodial threads are extruded through the cell walls. Fig. 151 represents part of a single filament highly magnified. Its sheath is thin; its squarish cells are marked off as sharply as though drawn with a ruler. Any one of them may divide to increase the length of the thread.

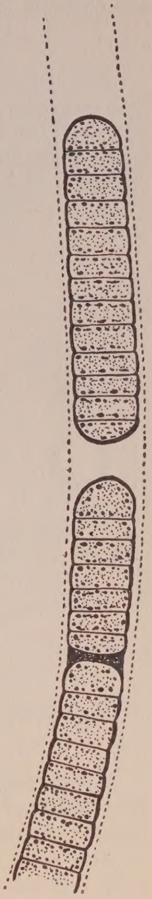

FIG. 151. — *Oscillatoria.* Single filament showing sheath and hormogonia.

There is doubtless considerable distribution of the plant through mechanical breaking of the filaments, but in addition to this method of spread *Oscillatoria* has evolved a mode of reproduction through the production of *hormogonia*. Short pieces of the threads are cut off by the death of certain cells, which gradually soften and disintegrate, setting the hormogonia free. Then they slip out from the parent sheath and proceed to develop into independent plants. This is a common method of reproduction for all the filamentous species.

C. NOSTOC AND THE HETEROCYST

This is another common blue-green alga (Fig. 152). It often grows attached to the stems and the leaves of water-lilies and other aquatic plants in the form of small green beads, though some species rest freely upon the bottoms of ponds in firm masses as large as small cherries. *Nostoc* also thrives upon wet soil or even upon wet shingles.

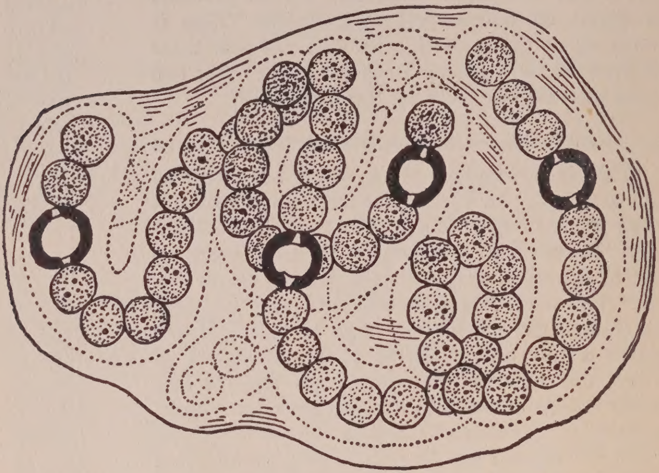

FIG. 152.—*Nostoc*. A small jelly-bead filled with coiled filaments which include prominent heterocysts.

When a fragment of the jelly is crushed and examined, the appearance is that of a mass of bead chains coiled together. Hundreds of filaments lie spirally twisted inside a common jelly mass which arose originally as a product of their joint activity. The individual bluish-green cells are bead-like, though here and there in the chains are intercalated the so-called *heterocysts*. The heterocyst is a peculiar body whose nature and function has long been a puzzle. It arises from a vegetative cell which enlarges slightly and develops a thicker wall and yellowish contents. There is usually a conspicuous simple pit at either end so that it can remain in connection with adjacent vegetative cells. No function has ever been satisfactorily proved for the heterocyst,

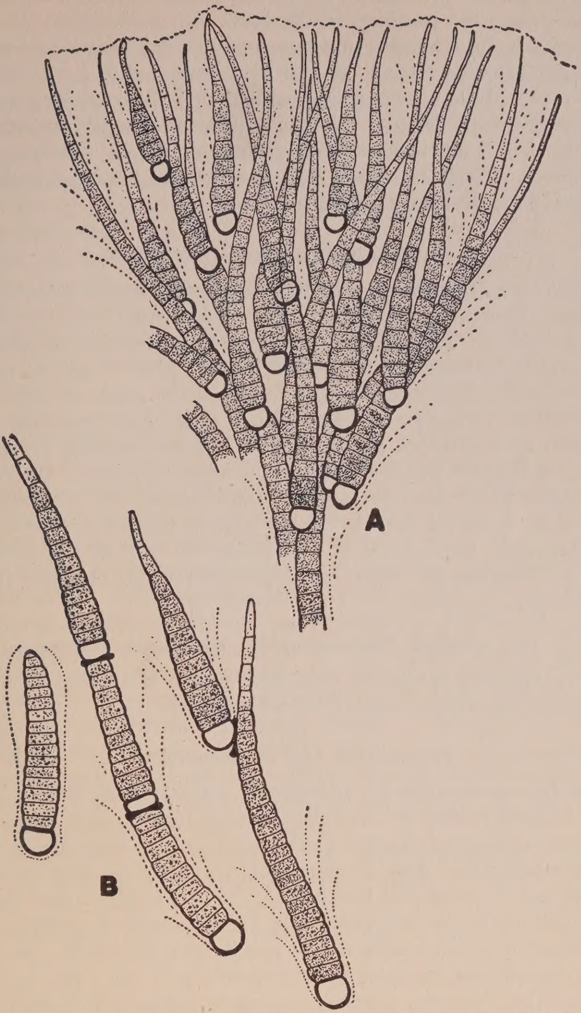

FIG. 153. — *Rivularia:* A, portion of the gelatinous mass flattened under a cover-glass; the tapering threads all arose by false branching; B, stages in the formation of a false branch.

though it has been variously regarded as a reservoir of food, a means for facilitating the breakage of the chain into hormogonia, or a reproductive body. The view that it represents a degenerative reproductive body is gaining ground. In 1910 it was reported that a heterocyst of *Nostoc* had been seen to split open and that the contents gave rise to a new filament. In 1911 this was confirmed for a different species, while in 1925 it was observed in three genera, *Nostoc*, *Anabæna*, and *Tolypothrix*. These extremely rare cases of germination may be interpreted as reversionary phenomena.

D. RIVULARIA AND FALSE BRANCHING

Rivularia will serve as one of the more complex representatives of the class. Like *Nostoc*, it grows in the form of small beads adherent to water plants. Fig. 153, A, illustrates the microscopic appearance of the contents of such a bead crushed into one plane beneath a cover-glass while Fig. 153, B, shows the details of the origin of one of its side members through a process which is called *false branching*. By this term we mean that a portion of a filament becomes set apart, commonly through the death of an adjoining cell, and it thereupon proceeds to pierce the surrounding gelatinous sheath and to grow outward as a lateral branch. If the process repeats itself over and over, the final appearance of the colony is that of a branching tree. In *Rivularia* the false branch generally starts out just below a heterocyst.

109. *General Features of the Blue-Green Algæ*

The preceding studies of particular genera will make more intelligible a general treatment of the whole group.

A. HABITATS AND DISTRIBUTION

The blue-green algæ are widespread, and the many genera grow under a great variety of conditions. They inhabit both fresh and salt water, particularly waters which have become contaminated with organic matter; they grow on mud-flats; they form slippery films on wet soil and on rocks and tree-trunks. The color of the Red Sea is said to be due to the blue-green alga *Trichodesmium erythræum*. In this instance the cells possess a high content of a carotin-like red pigment. Certain genera enter into symbiosis with the fungi to form lichens. The liverwort, *Anthoceros*, harbors colonies of *Nostoc* in its intercellular spaces, as does also the water-fern *Azolla*. *Nostoc* also lives symbiotically in the roots of cycads and in the mucilage cavities which traverse the petioles of the angiosperm *Gunnera*.

B. CYTOLOGY

The blue-green algæ like the bacteria, possess no true nuclei, yet recent studies have shown that the cells carry in their central region a mass of material which possesses many of the properties of chromatin and which is distributed to the new cells which result from the divisions. Fig. 154 shows the appearance of this material in the genus *Anabæna.* The black granules in the peripheral cytoplasm are masses of reserve food.

The pigments of the cell are two. Chlorophyll is present and is accompanied by a bluish compound called *phycocyanin.* There are no chromatophores, and the pigments seem to be spread evenly through the cytoplasm.

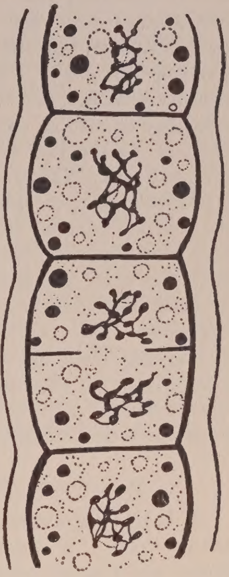

FIG. 154. — *Anabæna.* Portion of a filament highly magnified to show cytological detail of the blue-green algal cell.

C. SYMBIOSIS WITH BACTERIA

It has long been suspected that certain of the blue-green algæ, like certain of their relatives the bacteria, possess the power of abstracting nitrogen from the air. Recent experiments, however, have rerevealed the surprising fact that although sand cultures of blue-green algæ did increase appreciably in nitrogen as time passed, yet the algæ themselves are not responsible for the phenomenon. Their gelatinous sheaths are swarming with bacteria of many kinds, among which are found the familiar nitrogen-fixers such as *Azotobacter* and *Pseudomonas.* It is these symbiotic bacteria which are responsible for the gain in nitrogen.

As regards temperature range, the blue-green algæ resemble the bacteria in living under conditions which would be fatal to all other plants. No climate is too rigorous for them, and they vegetate profusely in arctic snow-pools where the water is rarely free from ice. They can dry out and lie for months frozen in snow and in the darkness of the polar night. Yet, on the other hand, *Oscillatoria* and *Nostoc* have been found in hot springs whose temperatures attained 90° C.

D. RELATION TO LIMESTONE FORMATION

In this peculiar habitat they are concerned with the formation of those deposits of brilliantly colored lime known as travertine. In limestone regions, too, they play a prominent part in the formation of similar calcareous deposits. Certain lakes have been studied whose waters were green and whose shores were covered with a bluish-green incrustation which also clothed the sticks and stones in the lake itself. It appears that certain filamentous blue-green algæ are largely responsible for this. They precipitate the lime in their gelatinous sheaths — an activity which seems to be partly physico-chemical. The solubility of calcium carbonate is enhanced by the presence of carbon dioxide. As the algæ rob the water of this gas in their photosynthetic activities, the dissolved calcium carbonate in the immediate vicinity is precipitated upon them. Recent studies of the phenomenon suggest that certain bacteria which live in the gelatinous sheaths of the algæ may play a part in the process. The filaments become so encrusted that the basal parts perish. The terminal parts, however, push forward, only to suffer a like fate later on. Thus the layer of marl is thickened. The calcareous concretions called "water biscuit" seem to originate from bits of stick or stone around which the radiating filaments of the algæ lay down concentric shells of lime. They often show a banded structure when sectioned and this may be an index of yearly growth increments.

E. THE MOST ANCIENT FOSSILS

It is this phenomenon which gives a key to the nature of certain ancient fossils. In the Proterozoic rocks of the northwestern United States and Canada occur nodular masses of concretionary limestone from which remains of filamentous algal plants have been isolated. These fossils were long known as *Cryptozoön* ("cryptic animal") and Eozoön ("dawn animal"), but they are now handed over to the botanist and are believed to be the product of blue-green algal action. The geologist Walcott has recognized some nine genera of them.* These are the oldest known fossil plant remains, and thus the blue-green algæ appear on the very first page of the fossil record. They are judged to have lived some 1,000,000,000 years ago. In connection with the algal cells of these calcareous remains there were found also the cells of bacteria, which are thereby assigned an equal antiquity.

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* C. D. Walcott, "Cambrian Geology and Palæontology," *Smithsonian Misc. Coll.*, LXIV, 1916.

F. ECONOMICS OF THE BLUE-GREEN ALGÆ

In comparison with the remarkable economic importance of the bacteria the blue-green algæ are almost negligible. Like most of the aquatic plankton their members enter into the dietary of aquatic animal life. One often sees under the microscope tiny transparent crustacea or worms whose intestinal tracts are gorged with blue-green or green algal cells. These small animals become the food of other and larger animals, and thus there is an ascending scale to the food-fishes. Cases of six degrees of this successive feeding have been remarked whereby organisms lay inside one another's digestive organs after the manner of a nest of Chinese boxes.

A second phase of economic importance rests upon the fact that the blue-green algæ sometimes pollute water supplies. They often accumulate in floating masses upon the water. Such material is called "water-bloom." There are cases on record where cattle and horses have been poisoned by it. In supplies of drinking water such algæ may become a decided nuisance, since they impart their characteristic and disagreeable odors. These odors are due to ethereal oils and they possess a remarkable penetrating power. Many other small algæ possess similar compounds. The oil which comes from the disintegrating cells of *Synura*, a tiny brown flagellate, can be detected in the proportion of 1 part to 25,000,000 of water. Copper salts are deadly poisons to algæ and they can all be controlled by treating the water with copper sulphate.*

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* Moore and Kellerman, Bull. No. 76, Bur. Plant Ind., U. S. D. A.

CHAPTER XVII

ALGÆ (PHYCOPHYTA)

110. *Introduction*

To the student of evolution no group of plants is of more interest than the algæ. Granted that schizophytes offer many astonishing morphological and physiological features, nevertheless they lie off the main highway of evolution, and the contribution which they can make to the elucidation of the problem of phylogeny of the higher plants is slight. Not so the algæ. It is to this group that one looks for the immediate progenitors of the land plants. In their diverse races we can find nearly all the morphological and physiological characters laid down which were destined to rise to full expression in the earth's dominant vegetation.

What is an alga? Well, the term covers such a heterogeneous assemblage of plants, so various in structure and reproductive device, that it can only be characterized upon an artificial basis as a chlorophyll-bearing thallophyte which possesses nuclei in its cells. The presence of chlorophyll sets the algæ apart from the bacteria and fungi; the possession of nuclei distinguishes them from blue-green algæ, while their thalloid nature serves to distinguish them from mosses and higher plants.

111. *Classification of the Algæ*

Not many years ago only three great algal classes were recognized. They were called respectively *Chlorophyceæ* or green algæ, *Phæophyceæ* or brown algæ, and *Rhodophyceæ* or red algæ. Sometimes the *Cyanophyceæ* or blue-green algæ were added to make a fourth class. This simple classification was maintained by selecting the single character of color as a basis for their separation. The *Chlorophyceæ* mostly possess the grass-green color of pure chlorophyll; the *Phæophyceæ* and *Rhodophyceæ* carry, in addition to chlorophyll, a brownish or yellowish and a reddish pigment respectively.

But as the science of algology developed, it became evident that the *Chlorophyceæ* included several groups of plants so diverse in structure that they ought no longer to be maintained in a single class. Likewise the class *Phæophyceæ* was seen to be an unnatural grouping. So, although the three classes are still maintained, they have been shorn of much of their greatness and have been forced to share their former territory with new classes of equal rank.

To the beginner, however, the refinements of systematics are likely to be more of a hindrance than a help, and so it seems best to stick to the easily remembered color lines, even though we admit that they include races of various phylogenetic origins. So we will consider the algæ under the heads of the Chlorophyte Line, Phæophyte Line, and the Rhodophyte Line.

I. The Chlorophyte Line

The group of chlorophytes or green algæ is a very old one — a veritable household of antiques — and it embraces remnants of diverse lines of evolution which doubtless differentiated early in the history of plant life. The members constitute the dominant green thallophytes which live in both fresh and salt water, though a considerable number have left the aquatic habitat and vegetate upon moist soil or even upon tree-trunks and rocks.

112. *The Flagellates as Parents of the Algæ*

The chlorophytes are believed to have evolved from a group of organisms known as flagellates. If we turn the microscope upon a drop of green-stained water, heavy with organic matter, we will usually see myriads of tiny organisms darting about. Some of them are pretty sure to be flagellates, which take their name from the fact that they propel themselves by means of the vigorous lashing movements of one or more whips (*flagella*) which they carry.

One of the commonest species is *Euglena viridis*, shown in Fig. 155, D, E. Its tiny one-celled body is spindle-shaped and it bears numerous bright-green chloroplasts in its cytoplasm. The chloroplasts enable it to carry on photosynthesis and to synthesize carbohydrate food out of water and carbon dioxide. And yet this decided plant character is associated with numerous features which one usually thinks of in connection with animal cells. *Euglena* possesses no rigid cellulose wall, and hence it can writhe vigorously in worm-like contractions; it bears a red eye-spot which is sensitive to light; it swims vigorously about, rotating on its long axis as it advances. So in this little organism we find a blend of plant and animal characters so intimately associated that we are unable to classify it definitely in either the plant or the animal kingdoms. The botanist calls *Euglena* a protophyte but the zoölogist calls it a protozoön. *Euglena* has many relatives; some are grass-green like itself, some are yellowish-green, others are pigmented golden-brown like the brown seaweeds, and there is even a genus (*Rhodomonas*) which bears a reddish pigment. Yet there exist also numerous colorless forms which must either carry on a saprophytic existence or must ingest solid foods like animals. Indeed,

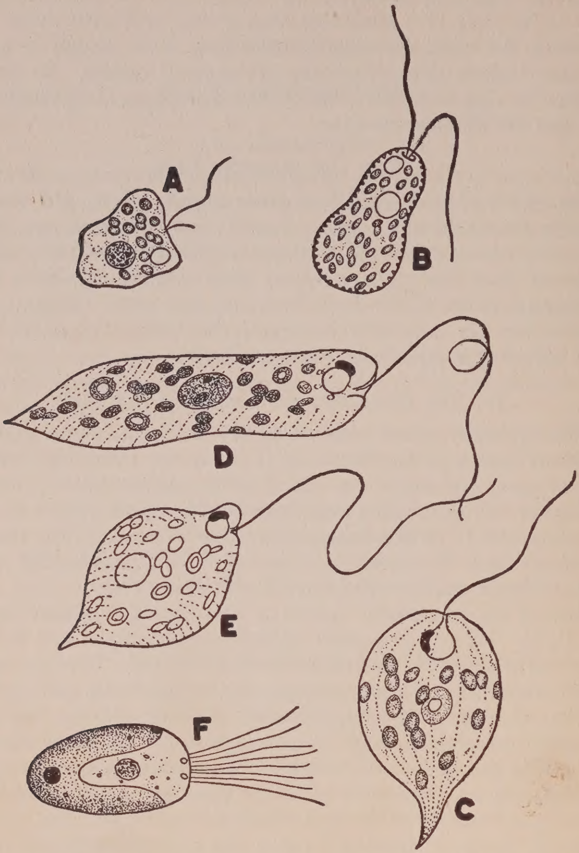

FIG. 155.—Various Genera of Green Flagellates: A, *Chloramœba;* B, *Vacuolaria;* C, *Phacus;* D, E, *Euglena* in the extended and contracted states; F, *Polyblepharis*. Redrawn Oltmanns after various authors.

Euglena gracilis is bright green when it lives in the light, but when placed in darkness it bleaches white and becomes saprophytic.

The flagellates generally reproduce by simply dividing lengthwise into two daughter cells. The process is repeated again and again till myriads of individuals have arisen from one original ancestor. A single parent cell can in this way soon people a whole pool of water. No flagellate ever lost an ancestor by death, since every flagellate is a part of that very ancestor.

But let us suppose that the products which arise from the successive divisions of a parent cell remain clinging to one another. The result will be a small plate or a sphere made up of flagellated cells. Such an evolutionary advance seems to have come early in the flagellate stock, and in this way the cell colony was brought into being. With the colonial life, something new and strange had come into the world. The colony is not merely the aggregate sum of its parts; its reactions are those of a unified organism and its sense of autonomy (the "I am" sense) embraces the whole cellular aggregation. We have already discussed this point in connection with the study of tissues in Part II. For, in another sense, the colonial flagellate is a simple tissue — it is "a collection of similar cells doing a similar work." From yet another aspect it corresponds to the early stages — the morula and blastula — through which the animal embryo passes.

From the naked-celled and decidedly animal-like flagellates there arose a group of motile organisms, both simple and colonial, whose cells are encased in cellulose coats. They were forging ahead along the plant line of evolution and are definitely relegated to the green algæ, yet they still bore the whip-lashes, the eye-spots, and even the contractile vacuoles so characteristic of their flagellate ancestors.

113. *Pandorina*

In Fig. 156, A, is represented *Pandorina*, one of the simplest of these colonies. It is not a rare species in collections of fresh-water algæ. *Pandorina* consists of from eight to sixteen biciliated cells each bearing a red eye-spot and a somewhat cup-shaped green chloroplast whose concavity is directed forward. The cells are held together by an investiture of colorless mucilage.

This little colony has two methods of reproduction. One is asexual and the other is sexual. In asexual reproduction the contents of any cell may divide by repeated mitosis into eight to sixteen small uninucleated pieces. They are motile bodies, and in many algæ they swarm out of the mother cell and give rise to new plants. They are called *zoöspores* and the cell which produces them is the *zoösporangium.* In *Pandorina,* however, the zoöspores do not swarm out separately from the zoösporangium, but adhere to one another instead, and form a miniature colony (Fig. 156, B) which finally escapes through a slit in the wall of the mother cell and assumes an independent life.

Sexual reproduction is carried on by tiny motile cells called *gametes* (*gamos* = "marriage"), which arise to the number of sixteen to thirty-two in the parent cells and are shed freely into the water. Here they proceed to unite in pairs and produce a smooth, red, motionless cell called a *zygospore*. It is known that gametes from different colonies unite with one another.

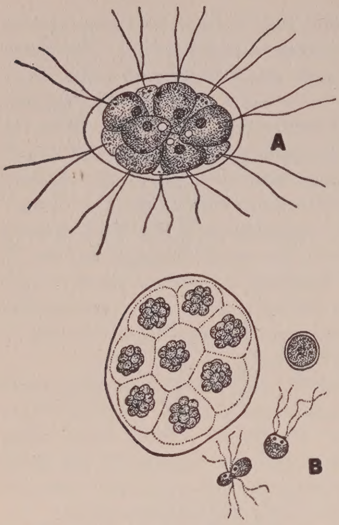

Fig. 156. — *Pandorina morum:* A, simple spheroidal colony of motile cells; B, eight daughter colonies have arisen. At the right are shown the slightly anisogamous gametes in conjugation and the zygospore which they produce.

In *Pandorina* they differ slightly in size, but in other and closely allied genera the microscope can detect no difference between them which would permit us to designate them as male and female. In such cases they are called *isogametes*, and the process of their union is known as *isogamy* or *conjugation*. The gametes seem to be only zoöspores which have taken on a new function, that of sexual union.

So in this humble plant we seem to witness the origin of sex cells. On the supposition that they are only small zoöspores it has been suggested that their pairing is really due to hunger. They are small and weak, and they proceed to eat one another. This is the "hunger theory of sex." That it is not wholly a wild notion is attested by the fact that algologists have succeeded in raising new plants directly from gametes when the latter were cultured in rich nutrient solutions. In other words, when they were well fed they did not practice cannibalism.

114. *Volvox*

The line of colonial motile algæ comes to its conclusion with the genus *Volvox* (Fig. 157). This queer organism has the form of a hollow, mucilage-filled ball plated over the outside with sometimes as many as 20,000 flagellated cells. It carries on both asexual and sexual reproduction. The asexual process results, as in *Pandorina,* in miniature colonies within the mother cell which finally burst through the wall. The sexual reproduction of *Volvox*, however, has advanced far beyond that of *Pandorina*, and its careful consideration will reveal facts and principles to which we shall often refer in subsequent studies.

The *Volvox* colonies are commonly of different sexes, though some species are hermaphrodite. Although they look just alike, the male colonies produce motile *sperm* or *microgametes* which arise in cells called *antheridia* or *microgametangia*, while the female colonies produce large, motionless *eggs* (*megagametes* or *oöspheres*) in *oögonia* or *megagametangia* (Fig. 158). Both are shed into the water. Then the active sperm cell seeks out the egg and unites with it. Since these gametes are not alike, they are known as *heterogametes* and their union constitutes *heterogamy;* or, if we prefer, we may say that the sperm fertilizes the egg. Since the female gamete is a distinct, motionless egg, the union may also be designated as *oögamy* and the product may be called an *oöspore.*

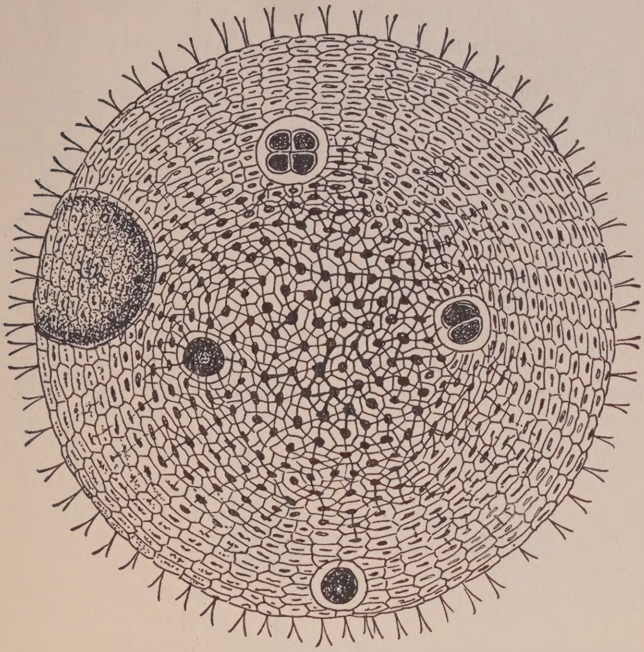

FIG. 157. — *Volvox globator.* The highest development of the volvocalian line. The colonies may rise to 20,000 cells in number, and there is considerable division of labor among them.

The physiological superiority of oögamy over isogamy is easily understood. It is clearly advantageous to the race if the young plants of the next generation can be given a head start and tided over the critical period of their infancy. Therefore a readily available supply of nutriment will be of great benefit. This is provided by the large egg cell, which becomes gorged with starch or oil. But hand in hand with increase in bulk goes an inhibition of its activity, to a final point when it gives up motility altogether. The sperm, on the contrary, retains its archaic active character.

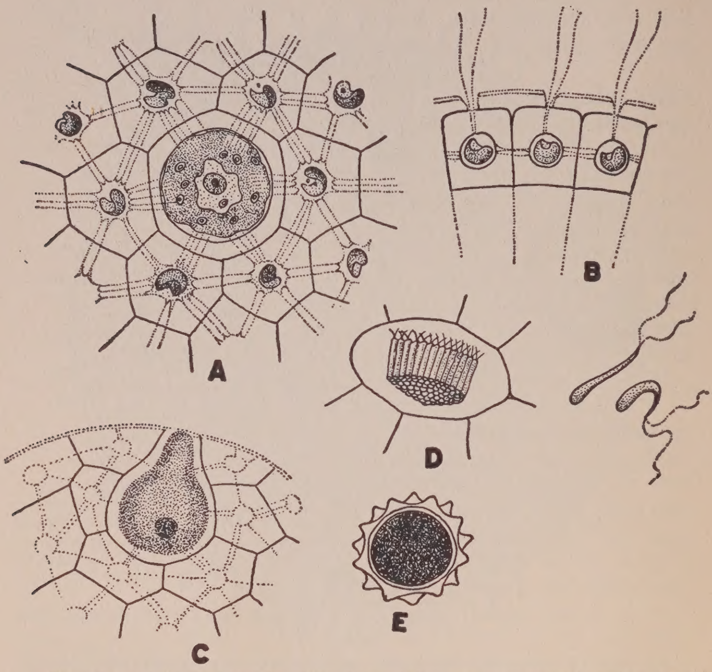

Fig. 158. — Histological Details of the *Volvox* Sphere: A, body detail in surface view; the cells are joined to one another by delicate cytoplasmic strands which traverse the thick gelatinous walls. The large cell in the middle is an asexual reproductive cell. B, body detail in sectional aspect. The body wall is but one cell thick, and copious mucilage accompanies the cells. C, oögonium and contained egg at the margin of the colony; D, antheridium with packet of sperm, with two free sperm cells at right; E, the prickly resting oöspore.

There is something very fundamental about these facts which are constantly associated with the conditions of maleness and femaleness.

In the oviparious vertebrates, even, the food supply for the embryo is stored in the egg; in the higher viviparous species placental nutrition permits the mother to feed the embryo directly. Furthermore, in the human species itself, we think of the female as the anabolic, less active, and conservative sex, whereas the male is actively katabolic and creative.

115. *The Terminology of Reproduction*

Let me summarize the matter which pertains to the sexual reproduction of *Pandorina* and *Volvox*. It should be grasped thoroughly, since it applies to group after group of plants which we shall consider in due course.

I. The reproduction of algæ may be asexual or sexual.

  A. In asexual reproduction the contents of a cell divides up into small motile bodies which are called *zoöspores* (*zoön* = "animal" viz., "moving" + *spore* = "seed"). They swarm into the water and after a short wandering life settle down and grow into new plants. In *Pandorina* and *Volvox* the products of the division of a mother cell cohere into little colonies and exit *en masse* from the mother plant.

  B. Sexual reproduction is carried on by gametes which seem originally to have been of the same nature as the zoöspores of which they are miniature editions. The gametes are produced in cells called *gametangia*. Their union produces a *zygote* (*zugon* = "yoke").

    1. The gametes may be identical in size, appearance, and function. They are then termed *isogametes*. They are borne in *isogametangia* and their union constitutes *isogamy* or *conjugation*. The product of isogamic union is a *zygospore*.

    2. The gametes may differ in size, appearance, and function. This is associated with difference in sex. The small, more active gamete is then called a *sperm*, or *microgamete*, and the large, slow-moving one is the *megagamete*. One is born in a *microgametangium*, the other in a *megagametangium*. Their union constitutes *heterogamy*. Often the megagamete loses its power of movement altogether, as it does in *Volvox*. It is then called an *egg* of an *oösphere*. Under these conditions the microgametangium is often called an *antheridium* and the megagametangium an *oögonium*. The process of union (zygosis) is termed *fertilization* and the product of the union is an *oöspore*.

I am well aware that this sounds pretty technical, but if the student will look closely to the derivation of the various terms he will experience no great difficulty in mastering them.

116. *The Four Main Lines of Chlorophyte Evolution*

With *Volvox* the first line of green-algal evolution comes to its close. As a successful type of plant body it was doomed to failure from the outset, but Nature rarely exhausts all her powers in one experiment, and along other lines she attained a greater success. Generally speaking, we can detect four types of body which have evolved among the algal races. These are:

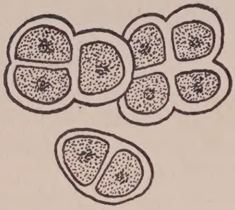

FIG. 159. — *Pleurococcus*, the Organism Responsible for the Green Stain on Tree-trunks.

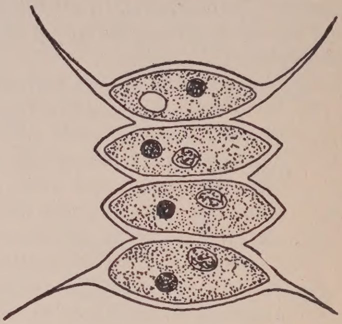

FIG. 160. — *Scenedesmus*, one of the Commonest Fresh-water Plankton Algæ.

1. Motile cells and motile colonies, already considered, and which ends with *Volvox* (order *Volvocales*).

2. Non-motile cells and colonies which drift passively about in the water (order *Chlorococcales*).

3. Tubular expansions which arise through the inflation of an original cell and finally result in a group of siphon-algæ whose bodies are multinucleate tubes without cross walls (order *Siphonales*).

4. Multicellular, filamentous bodies which arise from the repeated cross-septation and expansion of the products of an original cell and whose constituent units are uninucleate (orders *Ulotrichales* and *Conjugales*).

Let us now consider a few representatives from each of the second, third, and fourth groups.

A. SIMPLE NON-MOTILE CELLS AND COLONIES (CHLOROCOCCALES)

This order of green algæ is well represented in fresh water and embraces some very elegant little floating plants. A striking feature which many exhibit is a slender or elongate body form. Some are liberally provided with bristles. All these "slenderizing" devices are mechanisms designed to increase the frictional contact with the water. For since they no longer possess flagella, they must provide some other method of support or they will sink downward into the darkness. Not all the members, however, are free-floating; some attach themselves to other plants or to animals by means of gelatinous stalks or pads. One small group whose representatives are known collectively as *zoöchlorellæ* enter into symbiosis with certain sea animals, such as hydroids, and impart a chlorophyll-green color to their hosts.

Pleurococcus (Fig. 159) has abandoned the water entirely. Its little irregular colonies form the green stain which is often so abundant on tree-trunks, particularly upon their north sides. *Scenedesmus* (Fig. 160) and *Pediastrum* (Fig. 161) are two other genera which constitute beautiful, jewel-like objects when viewed with the microscope. Our figure shows that the zoöspores of the latter exit from the mother cell (zoösporangium) into a slime vesicle which is derived from the inner layer of the cell wall, where they come together and build up a colony which is a miniature replica of the parent.

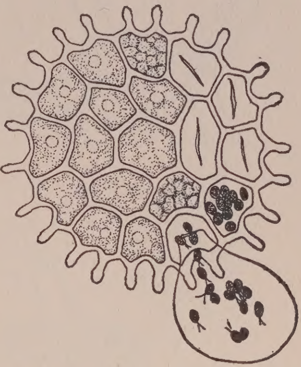

FIG. 161. — *Pediastrum*, Another Member of the Fresh-water Plankton. Zoöspores are escaping from a zoösporangium into a mucilaginous sac. Four cells have already discharged their zoöspores.

Hydrodictyon (Fig. 162), the water-net, is a most remarkable member of the group. Its frothy masses sometimes fill up ponds and ditches where the water is sluggish. The figure shows the curious structure of the thallus, of which the common name is sufficiently descriptive. These nets may grow to be even eight inches long. New nets arise through the approximation of zoöspores by their "finger-tips" inside the parent cell (Fig. 162, B). Both *Pediastrum* and *Hydrodictyon* carry on isogamous sexual reproduction. Stages of the process as it occurs in *Hydrodictyon* are represented in Fig. 162, C. Note that the zygospore germinates to produce several zoöspores. In many algæ these bodies swim away and grow directly into new plants, but in *Hydrodictyon* they are transformed into curious spiny cells from which the new nets finally arise (Fig. 162, D, E).

B. THE TUBULAR GREEN ALGÆ (SIPHONALES)

The tubular green algæ seem to have arisen, as we have said, through the inflation of an ancestral cell. In fact, that is exactly the manner in which each individual plant still comes into existence, and "ontogeny recapitulates phylogeny." The group underwent its greatest development in the warmer seas, and there are only a few of the simpler members to be found in fresh water. Probably the commonest genus, and the one which is usually studied in elementary

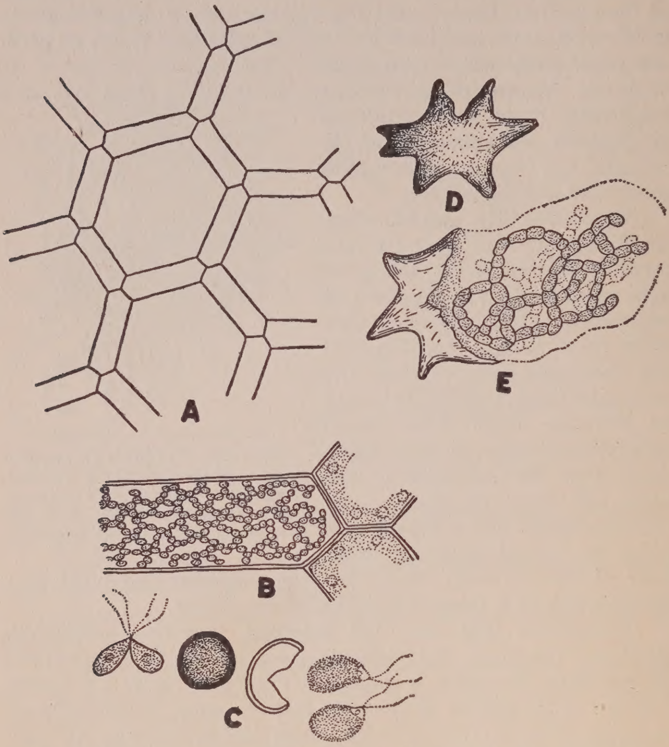

FIG. 162. — *Hydrodictyon*, the Water-net: A, portion of net magnified to show peculiar histology; B, young net arising through apposition of zoöspores inside the mother cell; C, isogamy, thick-walled zygospore, and subsequent escape of zoöspores; D, angular cell in which state the zoöspore comes to rest and subsequently forms the new net, E. (Redrawn various authors.)

courses, is *Vaucheria*. Its species are not all aquatic. In fact, the most familiar representative is the "green felt" which often grows abundantly upon the damp soil of flower-pots in well-lighted greenhouses.

If we make a water-mount of a bit of the emerald-green tangle, we shall find that it is made up of elongate and slightly branching worm-like threads similar to those shown in Fig. 163, and that there are no cross walls at all visible in its main axes. Spindle-shaped chloroplasts are abundant and lie close to the wall in a peripheral zone of protoplasm. Among them occur myriads of glistening oil droplets.

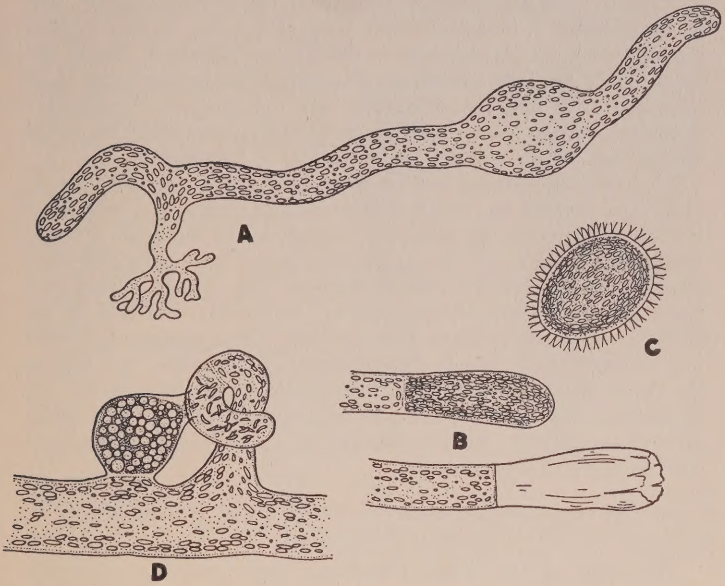

FIG. 163. — *Vaucheria*, the Green Felt: A, young plant with rhizoid (note absence of cross walls and presence of numerous chloroplasts); B, zoösporangium before and after liberation of the compound zoöspore; C, the zoöspore; D, oögonium with oil-filled egg accompanied by curved antheridial branch and terminal antheridium.

The land species of *Vaucheria* are well adapted to withstand drought and mechanical injury. If the soil begins to dry out, the contents of the threads may roll up into balls which develop heavy protective coats; if a thread is broken, the protoplasm may ooze out, form a wall around the liberated mass, and germinate like a spore.

Vaucheria carries on normally both asexual and sexual reproduction. Asexual reproduction of the aquatic species is by means of remarkably large zoöspores which are produced in zoösporangia borne at the tips of the tubes. The zoösporangium is set apart from the filament by a cross wall, and its complete protoplasmic contents is transformed into a single, large, multinucleate zoöspore (Fig. 163, B, C), which is beset with myriads of short, paired flagella (cilia) over its surface. It seems, in fact, to be a sort of compound zoöspore. Just as the filament is a multinucleate body and is not divided up into separate cells, so the zoöspore is likewise multinucleate and is not divided into separate zoöspores. The land-living species have often dispensed with motility altogether, and the common "green-felt" of the greenhouses bears only large motionless spores which are called *aplanospores* (*a* = "without" + *planasthai* = "wander").

In its sexual reproduction *Vaucheria* is oögamous and hermaphrodite. The oögonia are ovoid, slightly beaked bodies, and each gives rise to a single green egg filled with abundant food material. The antheridia are borne at the tips of slender, hooked branches which often stand in close association with the oögonia (Fig. 163, D). They give rise to numerous tiny, biciliate sperm. At maturity the beak of the oögonium opens and exudes a little mucilage. The sperm are discharged into the water; they swim to the oögonium (a film of rain or dew suffices for the land species) and enter bodily into it. A single sperm cell fertilizes the egg. Thereupon the latter becomes an oöspore and enters upon a state of rest. After a month or so it germinates and produces a new *Vaucheria* plant directly.

C. THE SEPTATED, FILAMENTOUS GREEN ALGÆ (ULOTRICHALES AND CONJUGALES)

The algæ of the orders *Ulotrichales* and *Conjugales* possess a unit of construction, the uninucleated cell, which is characteristic of the higher land plants. Their typical form of body is the filament composed of a chain of similar cells. In the simpler members the cells of the body appear almost identical in structure and in function, but in more advanced types vigorous branching is introduced along with a considerable differentiation of base and apex, so that beautiful arborescent forms may arise. There is a tendency also to assume the prostrate habit, and the creeping threads of some species are so closely appressed to one another that the plants come to look like flat plates or cushions.

In this group we find the common free-floating pond-scums which often occur in prodigious quantities in still waters. Here also stand many less conspicuous forms which grow attached to other plants and to sticks and stones. Let us consider a few of the more common representatives which the student is likely to pick up on almost any trip.

(1) *Spirogyra.*

The microscopic appearance of *Spirogyra* is probably better known to the non-botanist than is that of any other alga. For fifty years every generation of students has studied it as a representative of the group, though we must admit that it is one of the most atypical green algæ. *Spirogyra* is the pond-scum *par excellence*, and the dead waters of ditches usually become rank with it in summer time. It floats in large masses buoyed up by gas-bubbles and varies in color from vivid emerald to yellowish-green, depending upon its condition.

Even a simple inspection reveals the fact that the mass has a very slimy feel and that it is composed of myriads of slender threads. In fact, one of its names is "water-silk." The microscope resolves it into a simple chain of elongated, cylindrical cells all of which seem to be identical in form and all of which are capable of dividing so that the chain may be lengthened by the intercalation of new units.

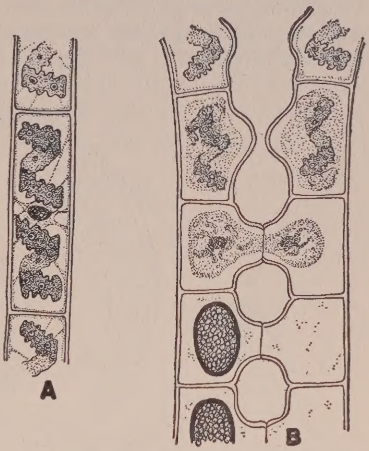

FIG. 164. — *Spirogyra:* A, portion of a plant whose cells carry but a single chloroplast; B, scalariform conjugation; two zygospores are already formed, while earlier stages of the process appear above.

The internal structure of the cells is peculiar (Fig. 164, A). The nucleus with its prominent nucleolus lies near the middle. It is enclosed by a thin jacket of cytoplasm from which streams out a set of slender cytoplasmic strands which radiate through the sap vacuole and link up with the cytoplasmic utricle. The nucleus with its strands resembles a conventional figure of the sun with its extended rays. A drop of iodine brings the system into clear view.

We have spoken of the chloroplasts of *Spirogyra* in another connection (Fig. 88). They are ribbon-like bodies with fimbriated edges and are coiled into spirals within the cell. They vary in number from one to twelve according to the species. At intervals in its course the chloroplast is studded with shining bodies called *pyrenoids*. They seem to be centers where the formation of starch goes on vigorously, and they are often ringed with starch granules.

Spirogyra belongs to an aberrant group of filamentous green algæ (order *Conjugales*). The plant is utterly without asexual methods of multiplication other than that which comes about through the breaking up of the threads.

In preparation for its sexual reproduction the threads become rather tangled and assume a yellowish color. Then every two filaments which happen to lie close to one another proceed to throw out projections from their constituent cells (Fig. 164, B). The protuberances meet tip to tip about midway between the two threads. At the place of contact the cellulose of both walls is dissolved, so that a tubular passage comes to connect each cell with its companion in the other thread. Then the cytoplasmic contents of the respective cells of one thread, which we may call the male, abandon their own positions, creep through the conjugation tubes, and unite with the contents of the companion to

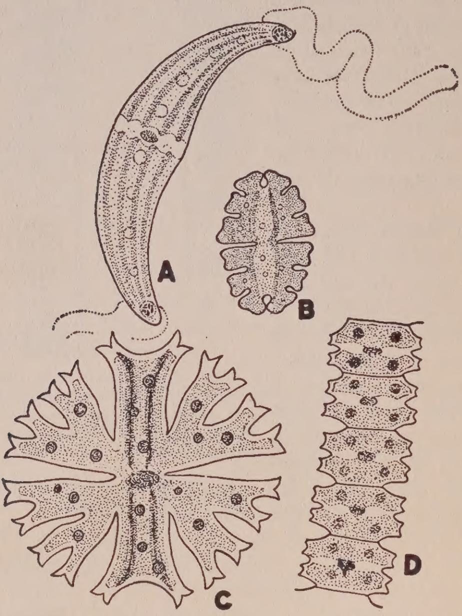

FIG. 165. — Desmids: A, *Closterium*, showing slimy exudate which moves the organism forward; B, *Cosmarium;* C, *Micrasterias;* D, *Desmidium*. (Orig. and adapted.)

which they are yoked. The cells of the male thread are thereby completely emptied of their contents. The double mass of protoplasm in each female cell now transforms into a globose or ellipsoidal brown zygospore. The female plants attached to the empty male threads and bearing chains of conspicuous brown zygospores are striking microscopic objects.

We see, then, that in *Spirogyra* the complete protoplasts of both threads are transformed into gametes. Since they are morphologically identical they must be called isogametes, and the product of their isogamy is a zygospore. If one wishes to draw a fine distinction, the situation may be described as one of physiological but not morphological heterogamy, since it must be admitted that one of the gametes in seeking the other behaves as though it were the male. The term *scalariform conjugation* is nicely descriptive of the peculiar "ladders" which result from the yoking of the threads.

Thus far in our studies of algæ we have paid no attention to the nuclear transformations which must accompany sexuality — a matter with which we must soon deal carefully in its various aspects because of its pertinence to the life histories of higher plants.

It is evident that zygosis must double the chromosome numbers in the nuclei and that a reduction division, comparable to the same phenomenon which we have observed in the angiosperms, must take place to prevent the summation of chromosomes in successive generations. When the zygospore of *Spirogyra* germinates, it is known that four nuclei appear. Three of them perish, and the fourth member becomes the functional nucleus which enters the young sporeling. These four nuclei are the outcome of a reduction division (meiosis) and each carries the haploid number of chromosomes (n), instead of the previous diploid number ($2n$). In many algæ all four nuclei function to produce four new plants, but *Spirogyra* seems to prefer to use all its food supply for the production of one well-nourished offspring.

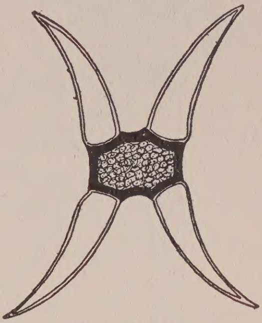

FIG. 166. — *Closterium* in Conjugation. A heavy-walled zygospore has been formed in the conjugation tube.

(2) *The Desmids.*

Closely allied to the conjugating filamentous algæ are the little water plants known as desmids, a few of which are represented in Fig. 165. They have long been the delight of the algologist because of their never-ending variety and their exquisite sculpturing. Sometimes they form filaments (Fig. 165, D), but more often they occur in the form of single, free-floating cells which assume various radiating or even lunate forms. The majority of desmid cells consist of two *semi-cells* which are connected by a narrow *isthmus*. A single nucleus lies at the isthmus, and there is commonly an elongated and plicated chloroplast in each semi-cell. Many forms exude strings of slime through pores in the wall and are enabled thereby to push themselves slowly forward over the substratum (Fig. 165, A).

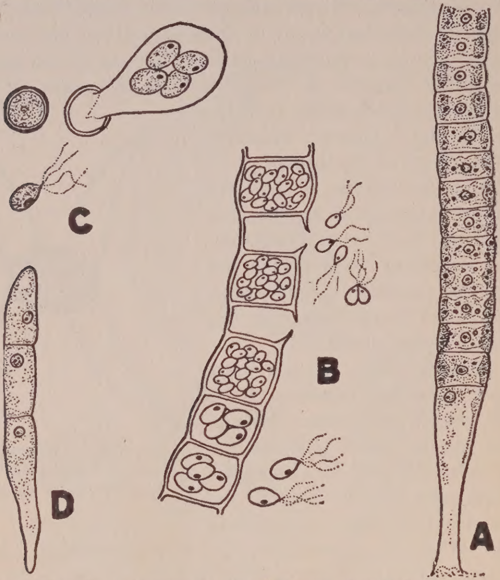

FIG. 167. — *Ulothrix:* A, filament in vegetative state, showing basal attachment; B, filament sending forth gametes above (two shown in isogamous conjugation) and zoöspores below; C, zygote in resting state and also germinating with zoöspores escaping into a slime vesicle; D, sporeling arisen from a zoöspore. (Adapted from various authors.)

Their method of reproduction is by conjugation and is carried on in a fashion similar to that of *Spirogyra*. In Fig. 166 are shown two yoked cells of *Closterium* with a zygospore held in the conjugation tube itself.

(3) *Ulothrix.*

As we have remarked, the conjugating algæ are aberrant members of the filamentous group. Closer to the main highway stands *Ulothrix* (Fig. 167). Its body is a simple unbranched filament, any one of whose cells may divide to increase the length of the chain. Its chloroplast is a green band which circles the cell at the equator. *Ulothrix* carries on both asexual reproduction by quadriciliate zoöspores, and sexual reproduction by tiny biciliate, isogamous gametes which swarm from the gametangia and unite in the water outside to produce a zygospore from which zoöspores are subsequently liberated. It is the latter which grow directly into new plants.

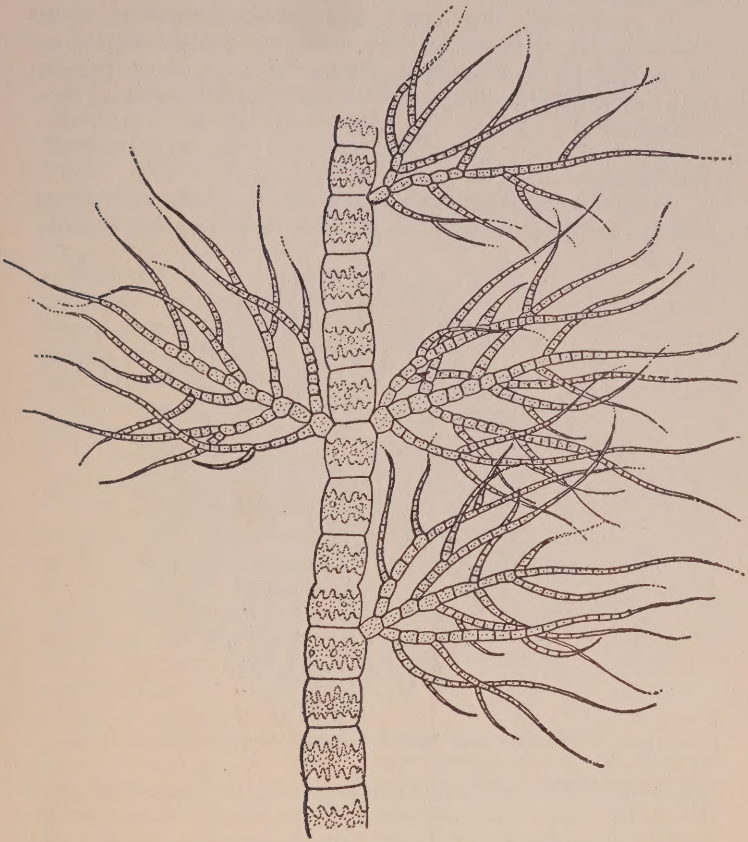

FIG. 168. — ***Draparnaldia***, the Highest Evolution of the Filamentous Green Algæ.

Ulothrix, then, has perpetuated the archaic reproductive method which characterizes the more primitive motile forms such as *Pandorina*.

(4) *Draparnaldia*.

In *Draparnaldia* (Fig. 168) is seen the highest evolution of the branching tree which was ever attained in this line of evolution, yet its reproduction by zoöspores and isogametes is practically identical with that of *Ulothrix*. *Draparnaldia* is to be sought in springs of clear, cool water.

(5) *Coleochæte*.

As regards reproduction, *Coleochæte* (Fig. 169) reaches the highest point among the green algæ. Its flattened thalli composed of radiating branches are often found appressed to the dead, submersed stems of cat-tails. Some of the cells generally bear long spines. In its vegetative body *Coleochæte* is simpler than *Draparnaldia*, but in sexual reproduction it has attained oögamy. During the summer time it reproduces asexually by zoöspores, but as autumn approaches, antheridia and oögonia appear at the tips of the branches (Fig. 170, A, B). A single sperm cell is liberated from each antheridium; it swims to the oögonium, enters through the elongate neck, and fertilizes the egg, which thereupon develops into a thick-walled oöspore. For its

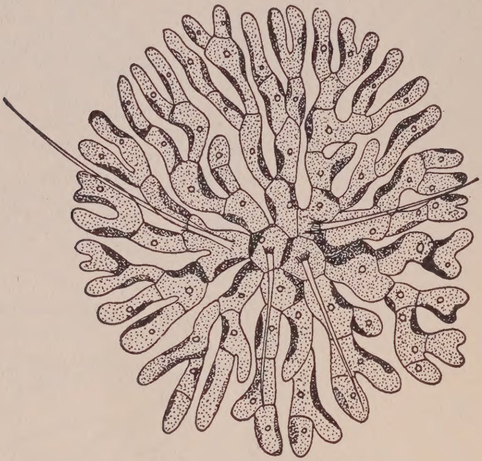

FIG. 169. — *Coleochæte soluta*, showing Habit of Thallus.

better protection, the surrounding twigs of the plant weave a cellular investiture about the oögonium. All winter long the oöspore rests in this condition. The following spring the diploid nucleus undergoes meiosis, thereby reducing the chromosomes to the haploid state. Then follow several other nuclear divisions, and finally a little parenchymatous body of about sixteen cells is built up inside the oöspore membrane. The oöspore finally bursts open, and from each of the sixteen cells a single biciliate zoöspore is set free to carry on the summer development of the plant. This little fruiting body is illustrated in Fig. 170, C. It has been vigorously discussed among botanists because of its possible bearing upon the life history of the higher plants.

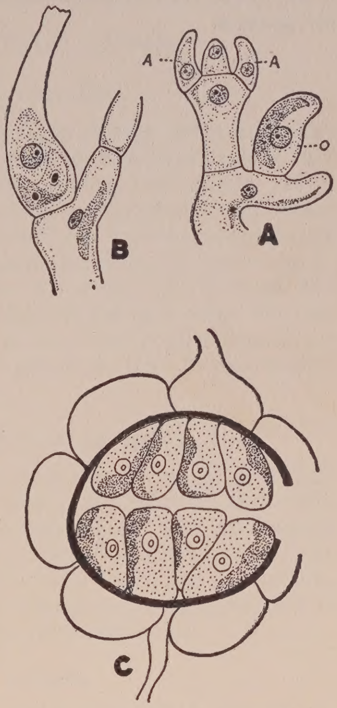

FIG. 170. — *Coleochæte;* A, reproductive branch bearing a young oögonium (O) and two antheridia (AA); B, oögonium in receptive condition; C, the germinated oöspore after the winter's rest. It contains an eight-celled body from which zoöspores are ultimately discharged. (Redrawn Oltmanns.)

A simple interpretation of the phenomenon may be suggested. It is the natural destiny of a zygote as it lies freely in the water to develop into a plant resembling its parent. This is what goes on in *Ulothrix* and *Draparnaldia* and in hundreds of other algæ. But in *Coleochæte* the egg is never discharged from the oögonium at all, and its full development is passed inside the maternal envelope. Consequently its growth appears to be stunted, and instead of producing a vigorous, green *Coleochæte* plant, it gives rise to a weak sixteen-celled body which liberates a set of zoöspores and then dies. But if this interpretation be correct, then the sixteen-celled body is also a *Coleochæte* plant and is strictly homologous with the green thallus of its parent. The offspring from the egg has been "encapsuled," so to speak, and the abnormal physiological conditions attending its growth have led to a profound change in its appearance. Yet the change appears to be no more fundamental than is the dwarfing of a geranium plant which has been kept in a flower-pot too small for its best development.

The sixteen-celled body which arises from the oöspore, whatever it may be, serves to increase the number of zoöspores which the plant can produce.

CHAPTER XVIII

ALGÆ (PHYCOPHYTA) (*continued*)

II. The Phæophyte Line

We come now to the line of thallophytic algæ whose chromatophores carry a brown pigment in addition to their chlorophyll, so that the members assume various shades running from golden yellow through brown almost to black. The term *phæophyte* covers a wide range of brown plants, and it is doubtful if it is more than a convenient term to assist the memory. Here stand various races of microscopic, golden-brown flagellates, lime-coated coccoliths, silica-invested diatoms, and the peculiar whirling peridines of the open ocean; but here also are included the rockweeds of the coast, and the great kelps of the ocean shores, which may attain a length of 300 feet. Truly a mighty and heterogeneous assemblage!

117. *The Flagellate Ancestry of the Brown Algæ*

Even as the green algæ seem to have arisen from the green flagellates, so the brown algæ merge away into a group of animal-like brown flagellates which inhabit both fresh and salt water and some of whose members are shown in Fig. 171. Like the green flagellates, they are shared rather impartially by both the zoölogist and the botanist. It will be seen that they, too, have developed colonial types, such as *Synura*, which is a close parallel to the green *Pandorina.*

118. *The Diatoms*

The most important group of microscopic unicellular phæophytes, and one which seems to have had a distant origin among the brown flagellates, is that of the diatoms. They are so abundant in natural water supplies that one can scarcely mount a slide for the study of algæ without finding their tiny "boats" scattered through it. Species of diatoms to the almost incredible number of 10,000 have been described, and specialists have devoted their lives to the study of them. They commonly live as free cells in water, though certain species hang together in mucilage-invested colonies or even in long chains. The cell wall is infiltrated with silica to such an extent that it has all the properties of glass, being perfectly transparent, rigid, and fragile,

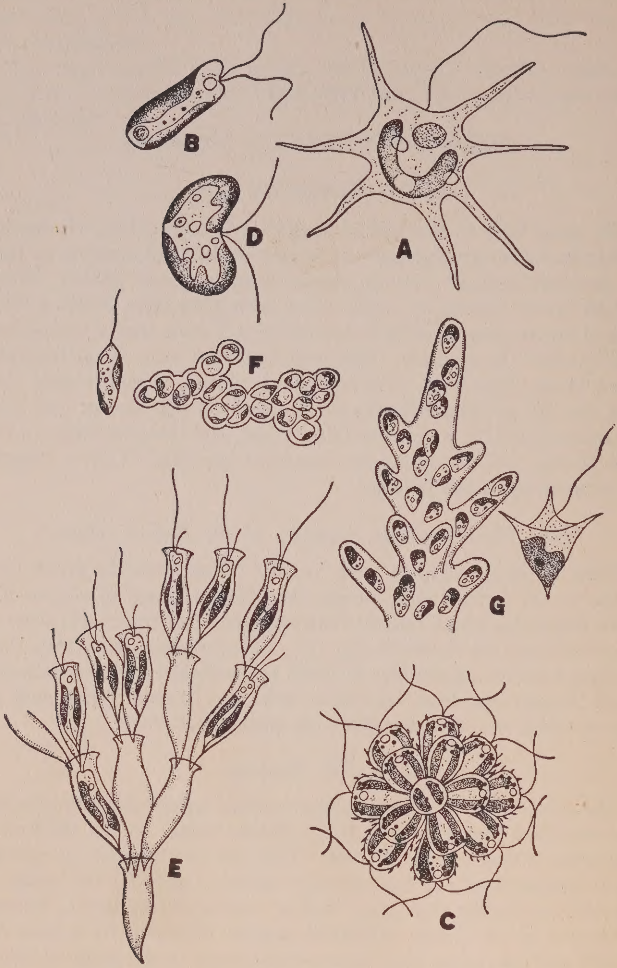

Fig. 171. — Representative Brown Flagellates: A, *Chrysamœba;* B, *Wysotskia;* C, *Synura;* D, *Protochrysis;* E, *Dinobryon;* F, *Chromulina;* G, *Hydrurus.* *Chromulina* and *Hydrurus* may pass into a resting state and become invested with jelly. (Redrawn Senn.)

and remaining undecomposed after the inner protoplasm has perished. Each cell (called technically the *frustule*) may be compared to a box with its cover, and it is described as made up of two *valves* (Fig. 172). The valves are commonly ornamented with dots, nets, stripes, or pits in bewildering variety among the various species. These are not mere surface embossings but are often due to complex modifications of the intimate structure of the wall itself — a matter about which little is yet known. The elongate, boat-shaped species generally possess a slit or *raphe* which runs lengthwise along each valve, and this is connected in some as yet unexplained fashion with the curious sliding motion which carries the diatom from place to place.

Inside this glass house is found the cytoplasm, in which are imbedded the plate-like, golden-brown phæoplasts. The product of photosynthesis is an oil of low specific gravity — a detail which doubtless assists them in keeping afloat in water.

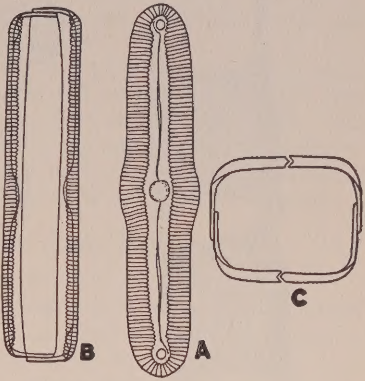

FIG. 172. — The Diatom Frustule: A, valve view of *Pinnularia viridis* showing central and polar nodules, raphe, and pinnate sculpturings; B, girdle view showing the two valves which fit together like a box and its cover; C, equatorial cross-section of the frustule.

A rather amusing feature is associated with their increase in numbers. In asexual reproduction the two daughter cells each carries off one of the parental valves of the frustule and generates the missing member anew. But the new valve is invariably shoved *inside* the old one — it is always the "box" and not the "cover" which is regenerated. In consequence the successive generations get smaller and smaller, till it looks as though the diatom grandchildren of various removes would finally vanish along the line toward zero. To save itself from this dire fate the diatom finally calls a halt in the process and throws off both valves. Then it may proceed to grow for a time without its coat of mail, or may conjugate with one of its fellows. In any case it is transformed into an *auxospore* (*auxein* = "to increase"), whereupon it sets out upon another cycle of diminution. A very few marine diatoms have been shown to possess motile zoöspores.

The diatoms of fresh water are usually elongate forms with feather markings (Fig. 172 and Fig. 173, B). Those of the sea are often shaped

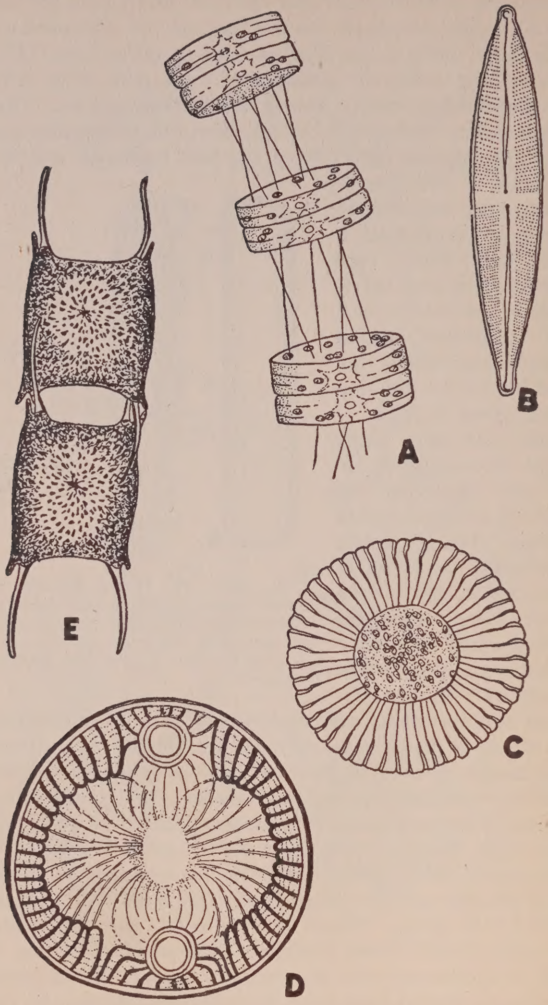

FIG. 173. — Representative Marine Diatoms: A, *Coscinodiscus polychordus;* B, *Staurastrum* sp. (this is a fresh-water species); C, *Planktoniella sol;* D, *Auliscus Rhipis;* E, *Biddulphia* sp. (Redrawn Oltmanns from various authors.)

like drums or cylinders and are sometimes marvelously ornamented, not only with pits and stripes but with spines and hairs which assist in keeping them afloat.

Diatoms like cool water and it is said that the bases of the ice-floes and bergs in the Arctic Ocean are brown with gelatinous coverings of diatoms. Along with other planktonic organisms they are of decided economic importance, since they form the basis for the dietary of food-fishes. The governments of the world have spent large sums of money in studying the diatom flora of the sea and calculating the laws which control its distribution and increase.

The dead shells of these small beings accumulate in enormous quantities at the bottoms of ponds and on the ocean floor in high latitudes, where they form what is called diatomaceous earth. This may consist of 80 per cent pure silica and contain 4,000,000 shells per cubic inch. Diatomaceous earth is used as an abrasive in scouring soaps and dentifrices, and sometimes as the inert base for dynamite.

119. *The True Brown Algæ* (*Phæophyceæ*)

A. INTRODUCTION

To the student whose early studies on algæ have been confined to the forms which are yielded by the fresh-water brooks and ponds, his first visit to the rocky seashore is a red-letter event. He has been familiar with the lifeless dried or pickled bodies of several seaweeds, but now here before him with their brown and red colors — so peculiar for a plant — their slipperiness and their smell, are the living rockweeds, the iridescent laminarias, and the delicate fronds of the brown, violet, and red forms. He gets the sense of ancient, far-off things as he begins to realize that for untold millions of years the ocean's great pulse has swept her waters twice each day over this tangled carpet of brown and red seaweeds.

If he brings forward his collecting jars, his microscopes and scalpels, the wonder deepens as he delves into the intimate structures and activities of these ancient plants.

B. ECTOCARPUS

Common along the Atlantic Coast, attached to the rocks or to larger algæ, are the tufts of several species of the genus *Ectocarpus* (Fig. 174). Beneath the microscope the plant shows itself to be of the habit of *Draparnaldia*, since it possesses a central axis and more delicate side twigs. Each cell carries a yellowish-brown chromatophore.

As regards their reproductive organs, the *Ectocarpus* plants are of two types, though their habits are practically identical. The fertile branches of one type bear small, pear-shaped, unicellular sacs which are the source of numerous laterally biciliate zoöspores (Fig. 174, D). Those of the other kind bear elongated tapering organs composed of myriads of tiny, cuboidal cells, from each of which a minute gamete is set free (Fig. 174, A, B). In other words, one sort of plant is a spore plant or *sporophyte.* It is asexual and reproduces by zoöspores. The other is a gamete plant or *gametophyte.* It is sexual and reproduces by isogametes.

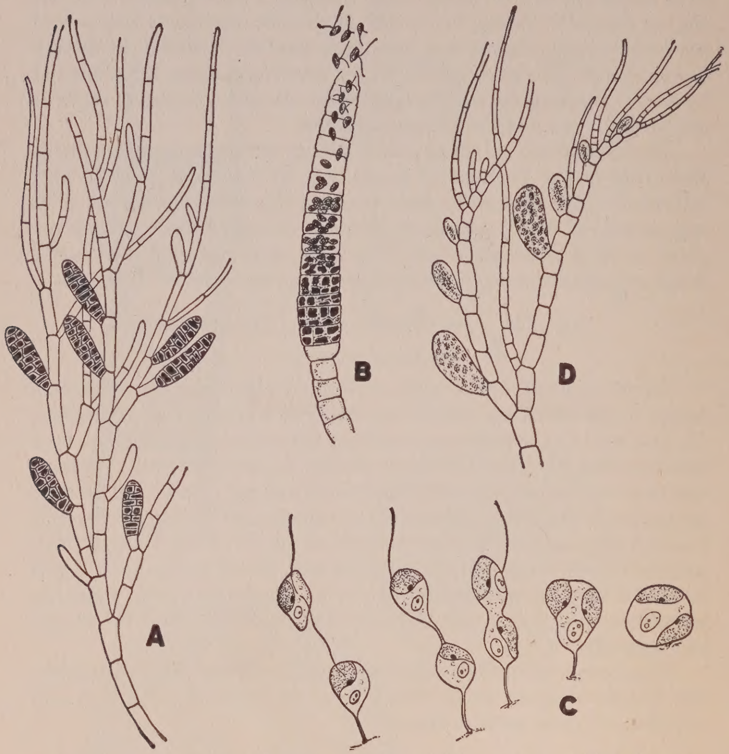

Fig. 174. — *Ectocarpus:* A, *Ectocarpus siliculosus* bearing gametangia; B, single gametangium enlarged to show escaping gametes; C, stages in conjugation of the gametes to form a zygospore; D, plant bearing zoösporangia.

Let us see how the two plants are related in the life history. When *Ectocarpus* plants are grown in aquaria under observation, it is noted that at about nine o'clock in the morning the sexual plants emit a cloud of tiny pear-shaped isogametes. Some of these swim immediately to the lighted side of the tank and come to rest. Then from all sides there hurries forward a swarm of seemingly identical gametes which cluster about the resting cells and begin a lively oscillating dance (Fig. 174, C). Finally one of the suitors unites with the resting cell, transforming it into a zygospore. In about twenty-four hours the zygospore proceeds to grow into a new *Ectocarpus* plant. From the behavior of the gametes it is evident that we are dealing with a slight physiological heterogamy. The gametes are invisibly differentiated into females and males, just as they are in *Spirogyra*, and it is the females that come to rest first and are sought out by the slightly more active males.

If there is no aberration in the life history, then the new plant which arises from the zygote will be an asexual one, and it will bear zoösporangia and produce numerous zoöspores which can grow directly into new plants. The plants which arise from the zoöspores will be sexual plants again. Consequently in the life history of *Ectocarpus* there is an alternation of gamete plants and spore plants, or gametophytes and sporophytes. This phenomenon is termed *alternation of generations*.

The key to this peculiar behavior is found in the history of the nuclei. The gametophyte constitutes the *haploid* generation; its nuclei bear the reduced (haploid or n) number of chromosomes. Its gametes are likewise in the n condition. The union of the gametes establishes a *diploid* zygospore *which proceeds to grow into a diploid sporophyte*, every one of whose nuclei contains $2n$ chromosomes. The young reproductive organs (zoösporangia) contain many $2n$ nuclei. As maturity approaches, each of these undergoes the chromosome reduction division (*meiosis*) and produces a tetrad of zoöspores. The zoöspores swarm out into the water and grow into new gametophytes. Let us put the idea in as concise a form as we are able. The gametophyte (n) produces gametes (n) which unite to form a zygote ($2n$). The zygote grows into a sporophyte ($2n$), in whose zoösporangia reduction divisions take place leading to the formation of numerous tetrads of zoöspores (n) which grow into new gametophytes.

C. THE TRIANGLE OF CYTOLOGY

There is a way of representing these cytological matters in the form of a diagram which the writer once found very helpful as an aid to interpretation. It is a bit technical, but that is a difficulty which lies in the nature of the subject and not in the diagram. The Figure may be designated as the *triangle of cytology*.*

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* O. F. Cook and W. T. Swingle, "Evolution of Cellular Structures," *Bull. No. 81, Bureau of Plant Industry* (Washington, 1905).

The three points of the triangle represent points in the life history of organisms where cytological changes occur. It is to be read in the clockwise direction. *Plasmogamy* means literally the union of two cytoplasmic masses of two gametes so that two separate nuclei come to lie inside a common protoplast. *Karyogamy* signifies nuclear union; after it is accomplished, the cell possesses a single diploid ($2n$) nucleus. Meiosis, as we know already, is the reduction division which normally results in four haploid (n) spores. It involves the temporary union of the chromosomes derived from both parents and the interchange of Mendelian determinants (genes). (See Chapter XV.)

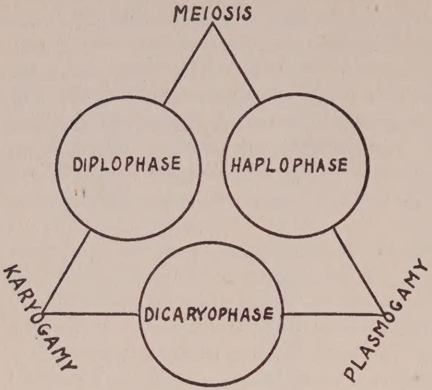

FIG. 175.—The Triangle of Cytology.

Now any one of the cell types generated at the points of the triangle can develop into a body of that type. Thus plasmogamy may be followed by a *dicaryophase* in which every cell of the plant bears two separate nuclei. This is particularly characteristic of certain fungi. More often, however, plasmogamy (union of cytoplasm) is followed directly by karyogamy (union of nuclei), and no dicaryophase appears at all. Karyogamy may be followed by a diploid ($2n$) phase or *diplophase*. Such is the condition in the sporophyte of *Ectocarpus*. Meiosis and the development of the resulting spores into new plants gives the haploid (n) phase or the *haplophase* again; such is the condition of the gametophyte of *Ectocarpus*.

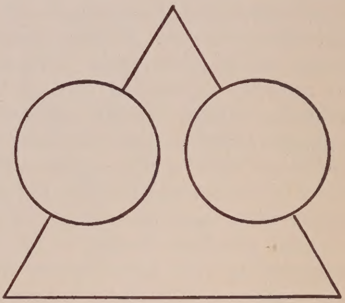

FIG. 176.—The Triangle of Cytology Applied to *Ectocarpus*. The haplophase (right) and diplophase (left) are represented by circles equal in size.

Hence if we diagram the life history of *Ectocarpus*, we shall have Fig. 176.

D. HOMOTHALLIC AND HETEROTHALLIC ALTERNATION OF GENERATIONS

We have seen that in *Ectocarpus* the thalli of the alternating generations look exactly alike, both being delicate branching brown algæ. This, however, is not true of all plants which possess alternation.

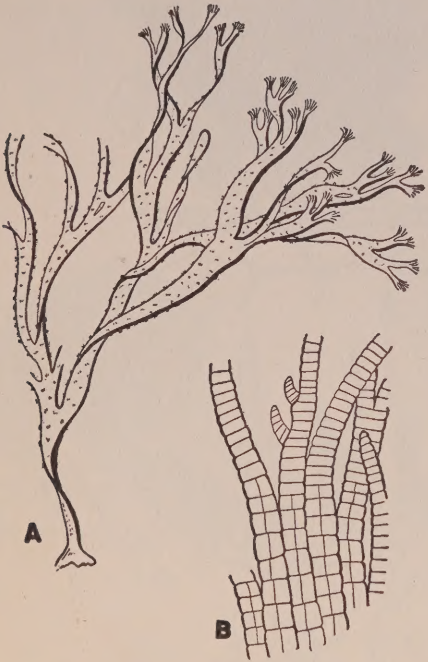

FIG. 177. — *Cutleria multifida:* A, habit of thallus; B, detail of growing margin of thallus (Redrawn Oltmanns [Thuret].)

In the diœcious *Cutleria*, for example (Fig. 177), the male and female gametophytes are both slitted thalli several inches tall and are identical in appearance. Yet Fig. 178 makes it evident that the reproductive bodies arising from the two plants are sexually differentiated. The megagamete or female gamete is many times larger than the microgamete. Fertilization establishes a zygote in the $2n$ condition.

Now comes the curious part of the story. The sporophyte which arises from the zygote is the creeping, flattened body shown in Fig. 179. Before the life history of *Cutleria* was fully known, this form was supposed to be a totally different alga and was placed in the genus

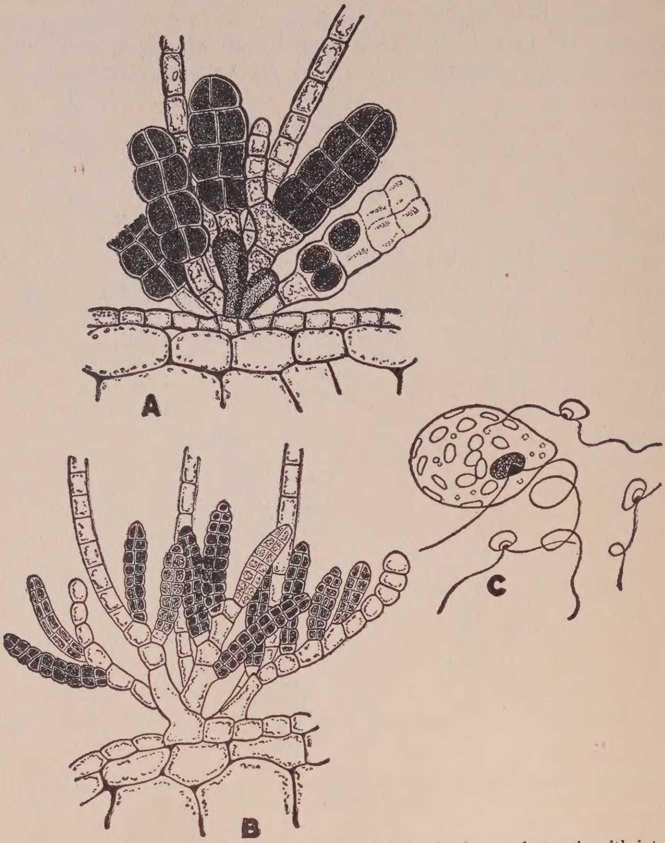

Fig. 178. — *Cutleria multifida*, Reproductive Details: A, cluster of oögonia with interspersed sterile threads; B, cluster of antheridia; C, megagamete accompanied by three microgametes. (Adapted Oltmanns from various sources.)

Aglaozonia. It produces quantities of zoöspores (Fig. 179, D). From careful cytological studies it has been determined that the *Cutleria* gametophyte bears twenty-four chromosomes in its nuclei, while the sporophyte ("*Aglaozonia*") bears forty-eight. The reason for the wide

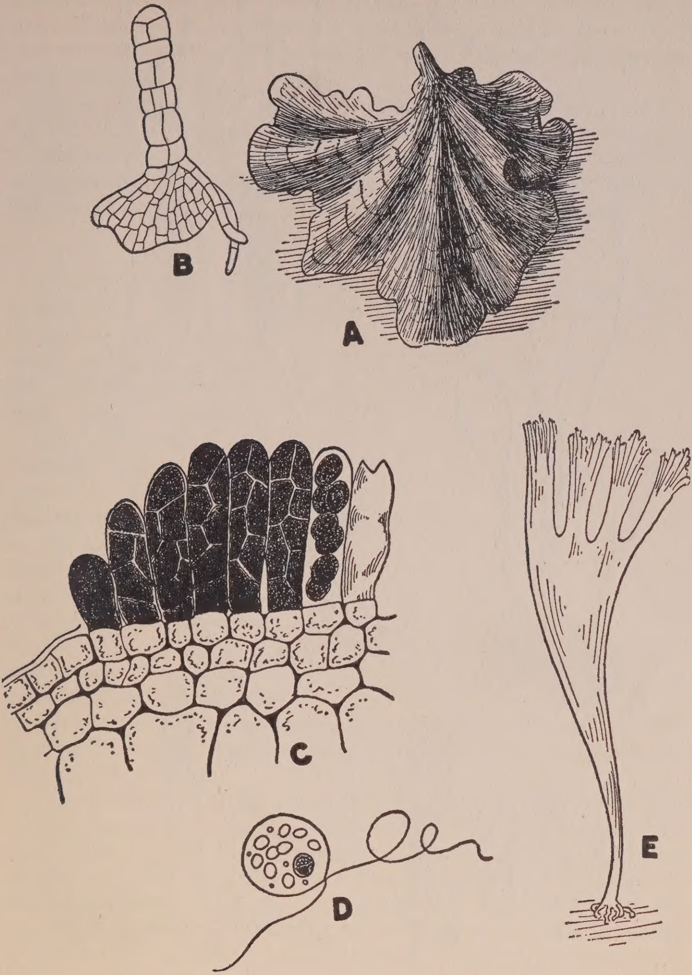

Fig. 179. — *Cutleria multifida*, the Sporophyte or Diplophasic Generation formerly called *Aglaozonia:* A, Habit of thallus; B, young plant derived from zygote; C, portion of cluster of zoösporangia; D, single zoöspore; E, young gametophyte (*Cutleria*) arisen from zoöspore. (Adapted Oltmanns from various sources.)

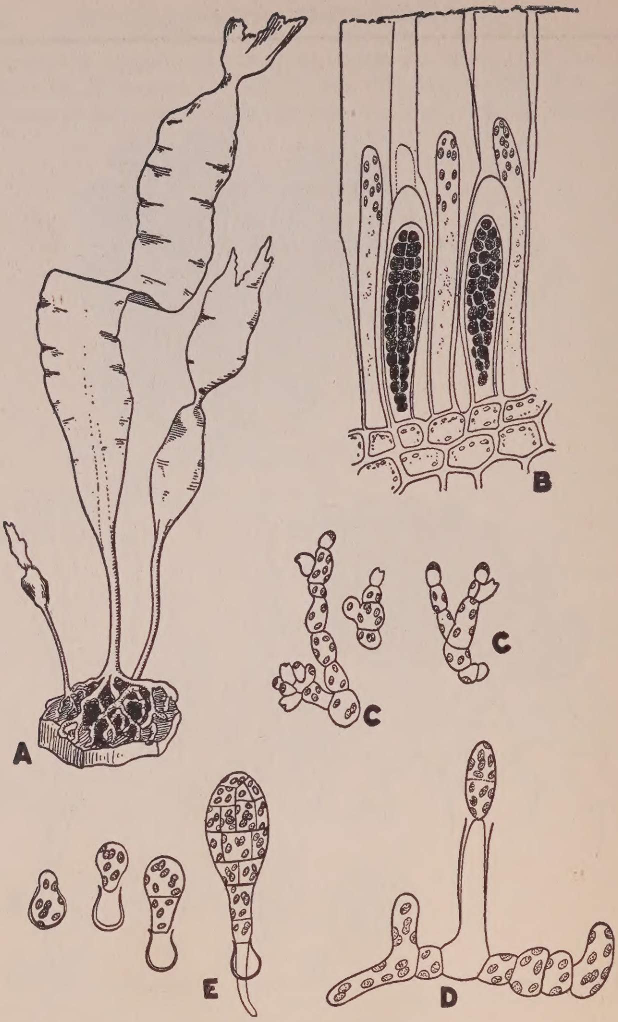

FIG. 180. — *Laminaria:* A, habit of plant of *L. saccharina* clinging to rock by means of holdfast; B, section through a fertile area beset with zoösporangia; C, male gametophytes with terminal antheridia; D, female gametophyte of *L. flexicaulis*. An egg has slipped out from the oögonium; it has been fertilized and has already divided once. It will develop into the sporophyte, A; E, young sporophyte of *Saccorhiza bulbosa*. In this species a single egg slips out from the zoöspore directly and after fertilization develops into the new sporophyte. Gametophytic tissue (haplophase) is completely suppressed. (B, redrawn Oltmanns [Kuckuck]; C, E. redrawn Sauvageau.)

divergence in form of the two generations is a highly debatable question. There is evidence that it is controlled by external factors and that the creeping sporophyte develops when external conditions are unfavorable to growth.

From comparison of the life histories of *Ectocarpus* and *Cutleria* it is evident that we may distinguish between two types of alternation of generations. When the alternants are equivalent in form, the phenomenon is designated as *homothallic alternation;* when they are different in form, the term *heterothallic alternation* is employed.

E. THE KELPS OR LAMINARIAS

One of the most interesting groups of algæ in the whole ocean is that which includes the kelps or laminarias. A common species, *Laminaria saccharina*, which grows just below tide level along the rocky New England Coast, is sometimes called the "devil's apron" (Fig. 180, A). Its brown leathery blades often grow to be several yards in length and are familiar specimens on the beaches where they are rolled in by the waves. The thallus tapers below into a firm cylindrical stalk which is anchored to the rocks by means of a strongly developed, root-like *holdfast.* The plant absorbs its food salts directly from the water and over its whole body.

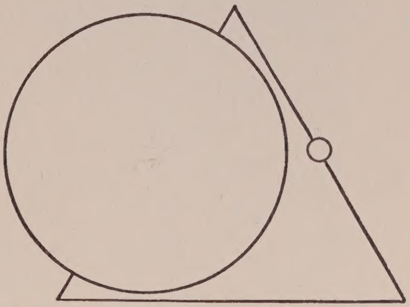

FIG. 181. — The Triangle of Cytology Applied to *Laminaria.*

The larminarias attain the highest anatomical differentiation of all the marine algæ. The great stalks exhibit a cortex, a meristematic zone which corresponds to a cambium and permits them to increase in thickness year after year, and, most remarkable of all, a central region possessing elongated, food-conducting cells which bear actual sieve-plates on their walls. The sieve-plates may even be sealed over with callus in autumn after the analogy of many angiosperm sieve-cells.

To see the laminarias at their best one should visit the northern shores of the Pacific Ocean. In these cool waters grows the giant kelp, *Macrocystis pyrifera,* whose thalli attain a length of 300 feet or more. They are shredded into blades which are supported by gas-filled floats and are anchored to the sea-bottom by cable-like stalks. Another large form is *Nereocystis*, which may grow to be 100 feet long and whose basal float may be six inches in diameter. In Pacific waters, too, are found the sea-palms *Postelsia* and *Lessonia.*

All the laminarias contain considerable quantities of potash and iodine. In France, particularly, they are gathered in quantity and burned for the extraction of these valuable substances. During the World War, a California powder company collected 621,000 tons of kelp for the extraction of potash.

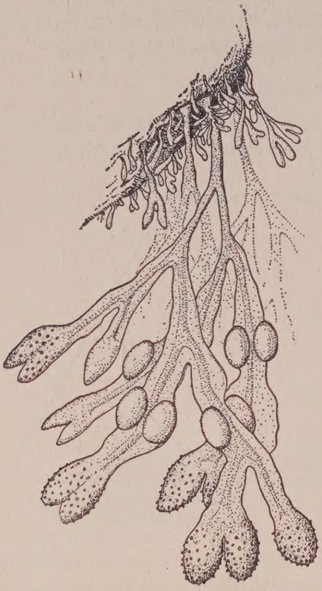

FIG. 182. — *Fucus* Plants of Various Ages Showing Method of Attachment, Swimming Bladders, and Fruiting Tips.

If the kelps impress the layman by their strange forms and large sizes, they impress the botanist by their remarkable life history. The visible plant is a sporophyte and sheds quantities of zoöspores from patches of zoösporangia which form on the surfaces of its blades (Fig. 180, B). Up to 1916 the full life history of the laminarias was unknown. In that year the French botanist Sauvageau proved that the *microscopic* plants shown in Fig. 180, C, D, are the gametophytes. They are of two sexes: the male gives rise to tiny biciliate sperm borne singly in microgametangia (antheridia), and the female produces ellipsoidal brown eggs singly in oögonia. From the fertilized egg the sporophyte again develops. This example of extreme heterothallism reaches its astonishing conclusion in *Saccorhiza bulbosa* (Fig. 180, E), where the zoöspore produces no vegetative body at all, and an egg slips directly out from it. We are obliged to say that the zoöspore has been transformed directly into an oögonium which produces its single egg and then perishes.

The representation of the history of the laminarias in diagrammatic form according to the triangle of cytology is shown in Fig. 181. The relative size of the circles indicates the relative importance of the alternating generations. One could hardly draw the haplophase circle too small.

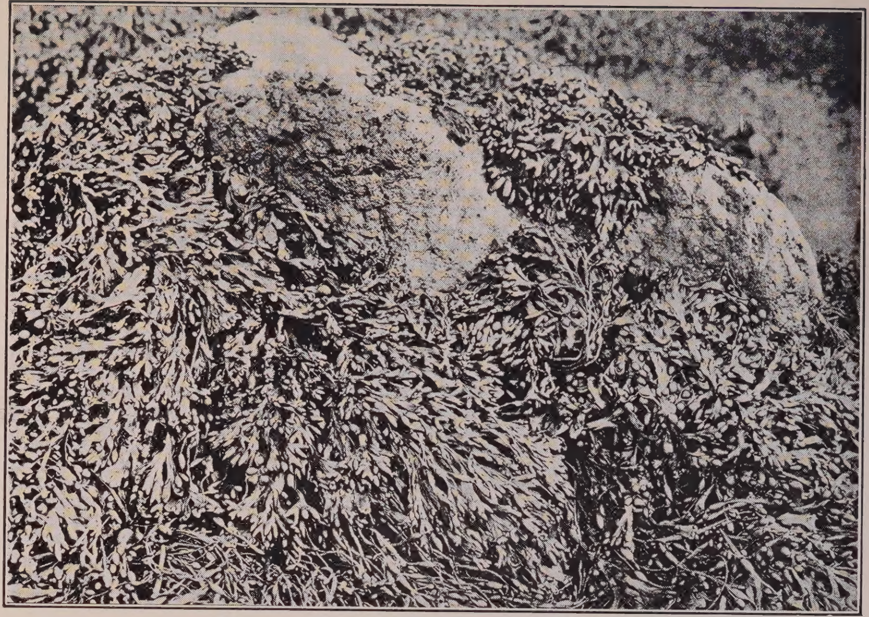

Fig. 183. — Typical Display of *Fucus* on Rocky Coast.

F. THE ROCKWEEDS OR FUCOIDS

Finally we come to the highest brown algæ, of which the rockweeds (*Fucus* and *Ascophyllum*) are familiar representatives, while the famous gulfweed, *Sargassum*, is another. They cling to the rocks of our coasts in shaggy, slippery masses which are exposed at low tide (Fig. 183). The leathery, forking thalli are firmly attached by basal holdfasts; many species bear bladder-like floats and as the tide comes in they are buoyed up by the rushing water.

The tips of the branches of the adult plants of *Fucus* are inflated, and the swellings are speckled with the openings of small flask-shaped cavities which are called *conceptacles* (Fig. 182). A tuft of hairs protrudes from the mouth of each one and numerous hair-pits are also scattered over the whole plant.

In the conceptacles are located the sex organs, which in section present us with the appearance indicated by Fig. 184, A. In this case we are evidently dealing with a diœcious species. The female conceptacles produce only oögonia, while the males bear only antheridia. Certain species of *Fucus*, however, are hermaphrodite, and eggs and sperm occur in the same conceptacle. An antheridial branch from a male conceptacle is shown in Fig. 184, B.

The gametes are discharged at maturity into the conceptacular cavity, and the mass of mucus in which they are imbedded oozes out through the opening during the time of ebb tide. The sperm mass is orange-colored; the mass of eggs is brownish. As the tide comes in the secretions are washed away and fertilization occurs outside the conceptacle.

For many years *Fucus* has been a classical plant in which to demonstrate to students the process of fertilization. The living algæ can be shipped on ice to inland laboratories. When bits of the brown- and the orange-colored slimes are mixed together in a drop of sea-water on a slide and placed beneath the microscope, the student will see the myriads of tiny, biciliate sperm hurry to the large, motionless brown eggs. The lashing of their cilia soon sets the eggs into lively spinning motion. Finally one sperm draws inward, and in about ten minutes it has entered the egg and the nuclei are united. Meanwhile the egg seems to throw off some substance which serves as a repellant to the other sperm, since they summarily hasten away.

Then the fertilized egg grows into a new plant which is exactly like its parents. But the thoughtful student is bound to reason thus: the *Fucus* plants produce gametes, therefore they are gametophytes, but theoretically the fertilized egg ought to produce a sporophyte. Still the text says that it grows into a plant "which is exactly like its

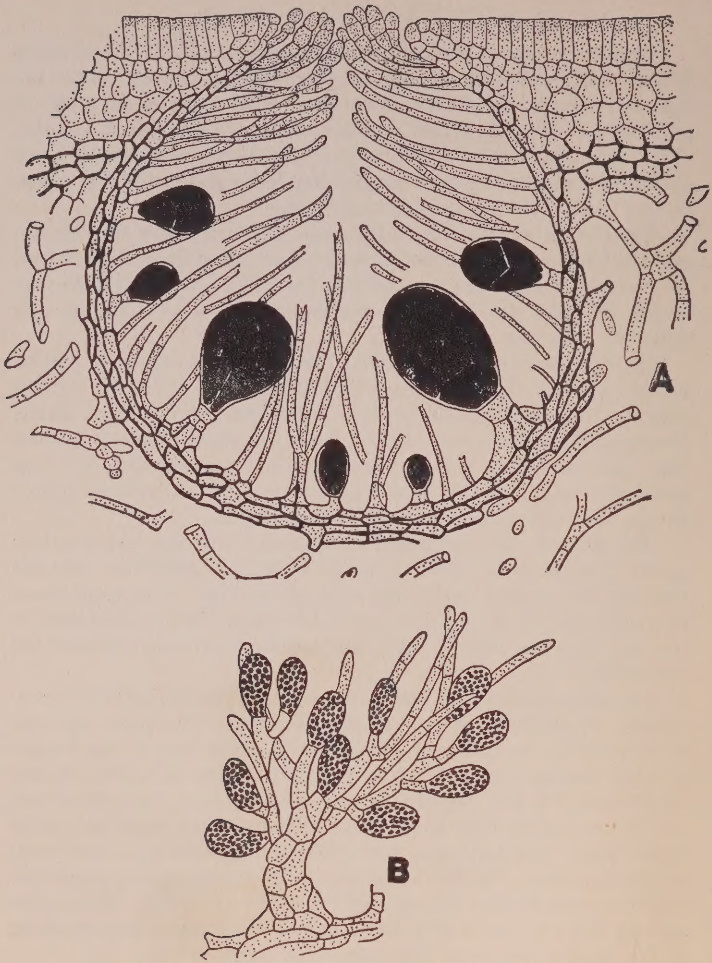

Fig. 184. — *Fucus:* A, female conceptacle in longisection showing delicate hyphal tissue of thallus; oögonia in various stages of development, some containing polygonal eggs. The hairs among the oögonia are called *paraphyses*. B, antheridial branch from male conceptacle.

parent." The key to this seeming paradox is supplied by the laminarias. *Fucus* has lost its gametophytes completely, and its cytological history is actually parallel to that of our own bodies. Its body is a $2n$ diplophase — truly a sporophyte, if diploidy be taken as the criterion of the sporophyte — but the reduction division, which in most algæ is followed by zoöspore production, is in *Fucus* succeeded immediately by gametogenesis. In *Saccorhiza* the zoöspores are set free and part of them develop into much dwarfed filamentous male plants which produce sperm cells in terminal antheridia. Another part of the zoöspores never develop any vegetative body at all but the whole protoplasmic content of the cell slips out in the form of a naked egg and is subsequently fertilized by a sperm.

In *Fucus*, however, the four zoöspores which arise from the reduction division do not escape from the reproductive sac at all; in fact they are represented by four free nuclei which divide at once homotypically so that either eight eggs or sixty-four sperm (by four successive mitoses) arise. It is these gametes which are expelled from the reproductive sacs and, in consequence, the reproductive secretions of the *Fucus* plants are eggs and sperm. This seems like a highly technical and theoretical interpretation, but there is cytological evidence to sustain it.

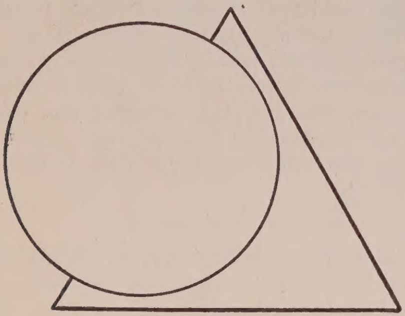

FIG. 185. — The Triangle of Cytology Applied to *Fucus*.

If we apply the triangle of cytology to *Fucus* we shall have Fig. 185, which is also applicable to our own bodies. The diplophase fills up the whole left-hand side, and there is no haplophase at all. So, if you and I were plants we would have to be called sporophytes. It is clear that conditions are completely reversed from what they were in *Pandorina* and in *Ulothrix*. There the whole life history is confined to the haplophase and fills up the right-hand side of the triangle.

G. ARTIFICIAL PARTHENOGENESIS

A rather remarkable experiment has been carried out with the unfertilized eggs of *Fucus*. If they be treated with weak acetic or butyric acid and then restored to normal sea-water, they develop into healthy plants which are *presumably in the haploid condition. And these young plants had no father* — they are virgin-born. Loeb has raised "fatherless frogs" from unfertilized frog's eggs treated similarly. The phenomenon is known as artificial parthenogenesis.

III. The Rhodophyte Line

120. *Introduction*

The red algæ share the tide-pools with the browns, though they tend to live in deeper water than do the *Phæophyceæ*. Their delicate fern-like thalli are well known to all who frequent the seashore. They possess a violet or reddish pigment (*phycoerythrin*) in their cells which usually masks the chlorophyll, though a few species (particularly a few which live in fresh water) are bright green in color. They stand quite sharply apart from other thallophytes, and their ancestry is unknown. Their reproductive activities are sometimes singularly complicated, and the careful study of them belongs to advanced botany.

121. *Nemalion*

Nemalion will serve to introduce us to the life history of one of the simpler members of the class *Rhodophyceæ*. Its thallus (Fig. 186) is a forking gelatinous body which shows itself under the microscope to be a compound structure consisting of separate parallel threads which run vertically through the plant and from which lateral bushy twigs radiate horizontally. The whole mass is held together by a secretion of thick jelly. The plants are of two sexes. The males bear small, densely branched, catkin-like bodies whose terminal cells are cut off to form minute, binucleate cells which function like sperm and are called *spermatia* (Fig. 186, B).

The female plants bear a kind of oögonium called a *procarp*, which consists of a basal swollen portion known as the *carpogonium*, where the egg lies, and an elongate terminal hair called the *trichogyne* (*thrix* = "hair" + *gune* = "woman") (Fig. 186, C).

The tiny, non-motile spermatia are washed among the female plants and become adherent to the trichogynes. Then the separating walls are dissolved and the contents of the spermatium are emptied into the trichogyne. One of its nuclei is carried downward to fertilize the egg. After fertilization the egg nucleus passes through meiosis.

This has actually been proved through chromosome counts. The male and female *Nemalion* plants bear eight chromosomes; the zygote bears sixteen and the reduction division now carries them back to eight. Following meiosis the nuclei increase in number, and from the carpogonium there is put forth a set of protuberances into which the

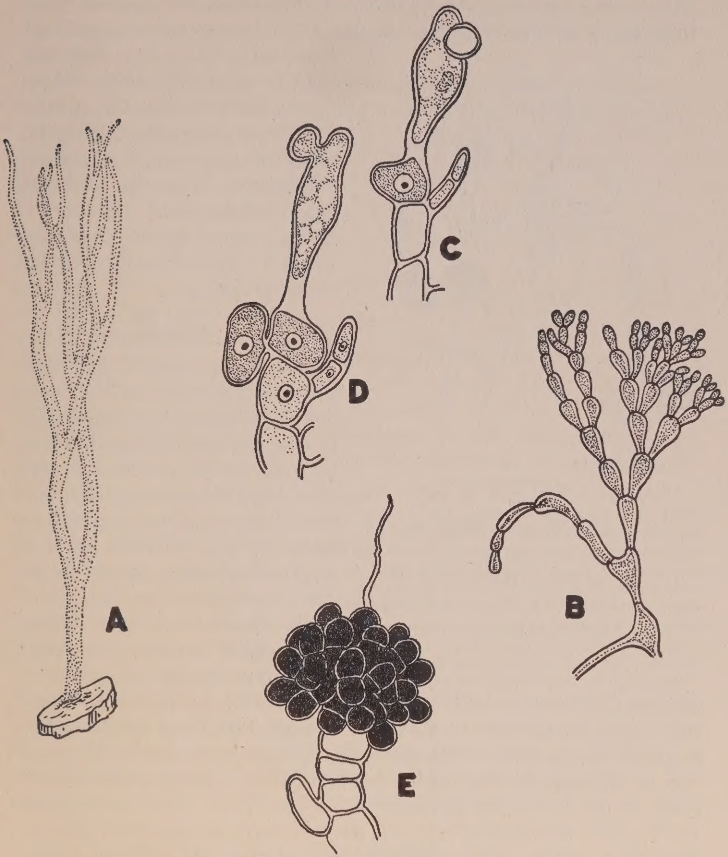

Fig. 186. — *Nemalion:* A, habit of the slimy, branching thallus which is traversed with myriads of slender branching twigs; B, antheridial branch of male plant; C, young procarp with spermatium adhering to trichogyne; D, the carpogonium is sending forth a carpogonial branch; E, cluster of mature carpospores. (C, D, Oltmanns [Kylen].)

haploid nuclei pass (Fig. 186, D). These finally develop into a forest of stubby, cellular branches whose end cells transform into rather large red spores. These constitute the *carpospores*, and the mass of them looks like a cellular ball (Fig. 186, E). The carpospores are finally set free in the form of naked, and slightly amœboid, bodies which grow into new *Nemalion* plants.

It will be evident that the mass of carposporic filaments which arises from the fertilized egg constitutes a true *carposporic plant* (*carposporophyte*) which lives parasitically upon its mother's body.

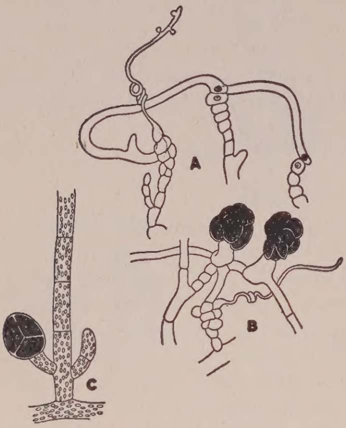

FIG. 187. — *Dudresnaya:* A, portion of female plant; the procarp bears a long, coiled trichogyne with spermatia adhering. From the carpogonium a long carpogonial thread has put forth. It has already effected a junction with one auxiliary cell, and its tip is about to unite with another. B, clusters of carpospores borne by auxiliary cells; C, portion of tetrasporophyte with tetrasporangium and tetraspores. (Adapted Oltmanns and Kny.)

122. *Dudresnaya*

For many years it has been customary to use another common coastal genus, *Polysiphonia,* to illustrate the difficult life history of the more advanced red algæ, but *Dudresnaya,* a Mediterranean genus, is better fitted to make it clear. *Dudresnaya* is a simple branching thread alga. The male plants produce spermatia similar to those of *Nemalion,* while the females bear procarps with long, coiled trichogynes. Fertlization is accomplished in a similar manner. But thereafter come complications. From the carpogonium there are put forth a few elongate carposporic threads which proceed to creep outward and to affix themselves to the terminal cells of side-branches which stand in the immediate neighborhood (Fig. 187, A). Each one of these latter constitutes an *auxiliary cell*, and within it the carposporic thread deposits a nucleus which is derived directly from the divisions of the fertilized egg. Then it moves forward to another auxiliary cell and repeats the process. From each auxiliary cell there is now put forth a set of carposporic filaments which develop terminal carpospores (Fig. 187, B), so that the mature mass resembles the carposporophyte of *Nemalion.*

But this is not the end of the story. The carpospores are shed from the parent plant and proceed to grow into new individuals which are identical in appearance with the sexual ones. But when they arrive at maturity they develop globose cells at the ends of short branches and convert the contents into four large, red spores (Fig. 187, C). These spores, from their definite number, are called *tetraspores*, and the plant which bears them is a *tetrasporophyte*. From the tetraspores comes the next sexual generation.

The nuclear basis for this life history has been successfully determined. When the fertilized egg begins to divide inside the carpogonium, the chromosome number is not reduced as it is in *Nemalion*, but the nuclei persist in the diploid condition just as they do under similar conditions in *Ectocarpus* or *Cutleria*. They are relayed into the carposporic threads, which grow outward and deposit them in the auxiliary cells. The latter are distinctly of the nature of nursing cells which have been impressed into service to receive the precious diploid nuclei and to assist in the development of the mass of carpospores. The haploid nuclei of the auxiliary cells never unite with the diploid nuclei brought to them by the carposporic threads. Now the carpospores, unlike those of *Nemalion*, possess diploid nuclei, and they produce another diploid generation — the tetrasporophyte. Reduction occurs in the tetrasporangium and the haploid tetraspores reëstablish the haploid sexual generation.

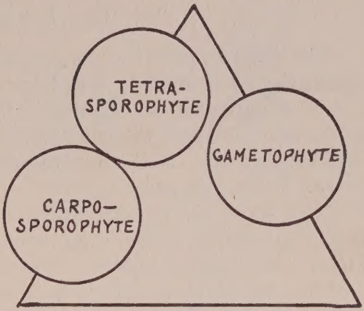

Fig. 188. — The Triangle of Cytology Applied to *Dudresnaya*.

So, in this complicated life history, we are concerned with three sorts of plants: (1) independent male and female gametophytes; (2) a parasitic carposporophyte which arises from the fragments of the fertilized egg and is nourished by auxiliary cells; and (3) independent tetrasporophytes. The situation may be diagrammed as in Fig. 188.

123. *Polysiphonia*

In the classic *Polysiphonia* the auxiliary cells cluster closely about the carpogonium and finally unite with it to produce a great nutritive fusion chamber for the nourishment of the carpospores. In this genus, too, a kind of cellular basket of sterile cells is developed around the carposporic mass and the whole structure is known as a *cystocarp*. The carpospores ($2n$) are set free and develop into tetrasporophytes ($2n$) which, in their turn, bear tetraspores (n) which reëstablish the gametophytic generation (n).

CHAPTER XIX

FUNGI (MYCOPHYTA)

124. *Introduction*

The fungi constitute a heterogeneous group of plants which are wholly devoid of chlorophyll and, in consequence, are forced to become either saprophytes or parasites. They are generally regarded as arisen from the algæ, though from what group or groups they came it is difficult to say. Both the green and the red algæ appear to be involved in their ancestry.

Here stand the familiar toadstools and puffballs, the smuts and rusts, the mildews, molds, and yeasts, as well as a host of delicate forms known only to the botanist. The division *Mycophyta* is of marked economic importance. It includes numerous destructive plant parasites which take a heavy toll from agriculture every year. Certain of the saprophytic forms, such as the bread-mold and the blue, green, and brown molds, are responsible for much food spoilage. Yet on the positive side of the ledger come the yeasts and the various edible mushrooms.

Three great classes are generally recognized. These are the *Phycomycetes*, or algal fungi; the *Ascomycetes*, or sac fungi; and the *Basidiomycetes*, or club fungi. The *Phycomycetes* seem to be of algal derivation, and a considerable number of them are still aquatic. The *Ascomycetes* are so called because their spores, which arise as the outcome of a sexual process, are borne in one-celled sacs called *asci*. The *Basidiomycetes* carry their sexually produced spores on small septate, or more usually non-septate, club-shaped filaments called *basidia*.

I. The Algal Fungi (Phycomycetes)

125. *The Transition to the Land*

From the standpoint of evolution the phycomycetes constitute the most interesting fungi, since a considerable number of them still live in the water like the algæ which are their probable ancestors. Moreover it is in this class that one can witness the conquest of the land by the fungi, since many of them have abandoned the water life and have developed remarkable and interesting adaptations to dry air and to inconstant water conditions.

We will deal with two representatives of the *Phycomycetes*. One of them grows only in the water, and the other is confined to the land.

A. THE WATER-MOLD (SAPROLEGNIA)

To get material of *Saprolegnia* for study it is only necessary to bring a jar of pond water into the laboratory and to throw into it a few dead flies or a fish head, or even pieces of boiled egg-white, and wait a few days for developments.

(1) *Zoösporic Reproduction.*

Gradually a white halo of filaments begins to appear around the organic matter (Fig. 189, A), and by the time the odor of the culture begins to "beggar description," one can see that the filaments are whitened for a few millimeters backward from their tips. Under the lens the whitened tips are discovered to be clavate zoösporangia in various stages of development. They arise from threads which run into the rotting substratum and are full of streaming, multinucleate protoplasm. This branching web of fungus threads constitutes the *mycelium*, and any single strand of it is called a *hypha*. The hyphæ of most of the phycomycete fungi possess no cross walls. They are, in fact, cytologically parallel to the threads of the siphonalian green algæ.

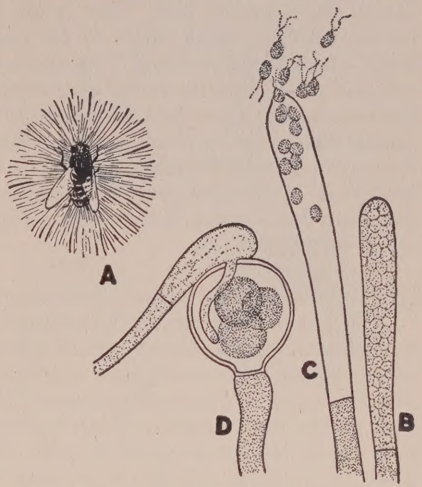

FIG. 189. — *Saprolegnia*, a Water-Mold: A, decaying fly surrounded by a halo of hyphæ; B, C, zoösporangia immature and mature; D, oögonium containing three eggs, with approximated antheridium which has sent in a fertilization tube.

Careful study will show that the protoplasm in the zoösporangia cleaves into uninucleate pieces (Fig. 189, B) which gradually round up and develop into biciliate zoöspores. Then they are expelled from the tip of the zoösporangium (Fig. 189, C) and swim actively away.

(2) *Sexual Reproduction of Saprolegnia.*

Saprolegnia also carries on oögamous reproduction. The oögonia are spherical bodies which are borne on shorter hyphæ than are the zoösporangia. They are visible to the naked eye as white specks close to the substratum. Each contains from one to as many as forty eggs, according to the species (Fig. 189, D). The antheridium is an elongated, club-shaped filament which may arise on the same or on another plant. It creeps to the oögonium, presses up against it, and then puts forth a slender branch, called a *fertilization tube*, which pierces the oögonium wall. Once inside the oögonium it sends out several branches which move to the eggs and effect fertilization. Nuclear fusion occurs at once. Then the zygote develops a two-layered wall and passes into the state of a resting oöspore. In *Saprolegnia*, therefore, motile sperm have been completely eliminated and the cœnocytic mass of sperm-plasm is carried through a fertilization tube to the eggs by its own streaming motion. It is obviously a more precise method of fertilization than the archaic scheme whereby the free sperm are discharged into the water, a scheme in which a great wastage is certain to occur.

(3) *Ecological Transformations Incidental to Land Life.*

Allied to the water-mold, *Saprolegnia*, are other genera, such for example, as *Pythium*, some of whose species still cling to the ancient water habitat, while others have migrated to the land and have become parasites and saprophytes upon land plants. They offer a most interesting ecological problem for our study and contemplation. It is clear that the zoösporic reproductive mechanism is a device which can function only in the presence of water. When the algal fungi set out to conquer the land, they were immediately faced with this water-problem, which they solved in an ingenious and admirable fashion. They transformed the sporangium itself into a small dry spore or *conidium* which could be easily detached and spread about by air currents. Then to keep up a large enough supply of reproductive bodies, they evolved the ancient sporangial stalk into a branching "tree" whose every tiny twig bore the transformed sporangia. In this way arose the group of the downy mildews. Familiar examples are the mildew of the grape and of the squash and the destructive late blight of the potato.

We have seen that *Saprolegnia* had already given up the formation of free swimming sperm and that its egg is fertilized by a fertilization tube which pierces the wall of the oögonium. Such a method of transferring the sperm to the egg was admirably adapted to land conditions, and most of the downy mildews have retained it. They generally develop their thick-walled oöspores in the autumn and pass the winter in that condition.

There is, however, a group of algal fungi which produce no eggs but carry on isogamous conjugation instead. The commonest of these forms is the bread-mold.

B. THE BREAD-MOLD (RHIZOPUS)

Among the smaller filamentous fungi none is better known to the layman than the bread-mold, *Rhizopus* (Fig. 190). To get a luxuriant culture for study one need only place a piece of bread in a moist chamber. In a few days it is covered with a delicate, cobwebby mycelium from which arise numerous, upright, tufted stems which carry tiny white or black capsules at their tips. A simple lens, even, reveals the fact that the cobwebby mass is composed of myriads of fine, branching, colorless threads just as it is in *Saprolegnia*. The hyphæ are anchored by tufts of tiny brown *rhizoids* which digest the organic constituents of the bread and keep up a vigorous absorption. The mycelium spreads about after the analogy of a strawberry plant by sending out slender stolons from its points of anchorage.

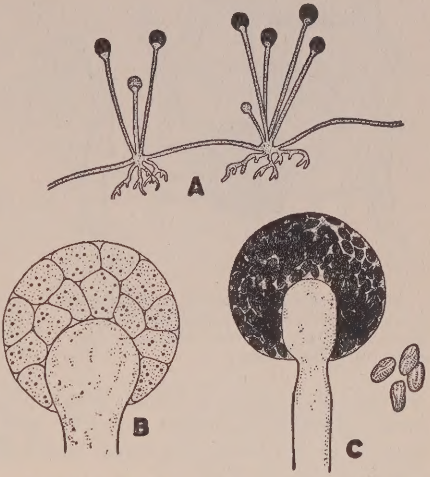

FIG. 190. — *Rhizopus nigricans*, the Bread-Mold: A, representation of the stoloniferous habit of the fungus; B, primary cleavages of the sporangial contents; C, mature sporangium and spores. (B, redrawn Harper.)

Under the compound microscope the hyphæ are found to be tubular and full of vesicular protoplasm; they possess no cross walls — a feature which is highly characteristic of all the algal fungi.

The stalked capsules are called sporangia (Fig. 190, C). When mature they are found to be filled with hundreds of minute black spores. Into each sporangium there rises a protrusion known as the *columella*. It is worthy of note that the production of myriads of tiny, dust-like spores lifted into the air upon stalks is an adaptation to the conditions of land life. In taking to the land *Rhizopus* gave up the motile zoöspore for the dry, powdery, reproductive body which is homologous with it. Every breath of wind scatters the spores broadcast, and they are a normal constituent of dust.

When the spore reaches favorable conditions of food and moisture, the outer coat (*exosporium*) cracks open and the inner coat (*endosporium*) protrudes as a delicate first hypha which proceeds to spread over the substratum in the form of a richly branched mycelium.

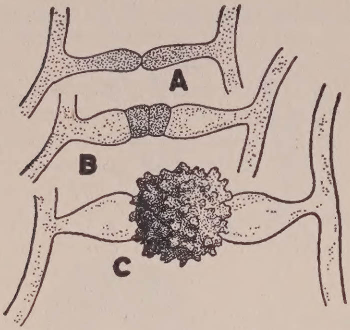

FIG. 191.—*Rhizopus* in Sexual Reproduction: A, approximation of fertile hyphæ; B, differentiation of gametangia; C, mature tuberculate zygospore. (Redrawn Brefeld.)

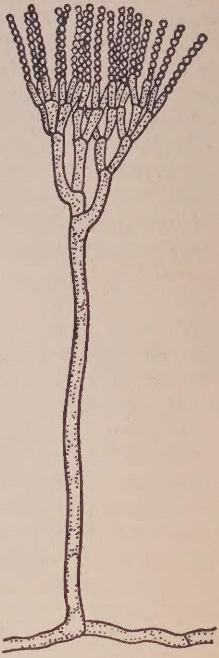

FIG. 192.—*Penicillium*, showing Conidiophore with Conidia.

Rhizopus also carries on sexual reproduction in a fashion which recalls the scalariform conjugation of *Spirogyra*. Fig. 191 shows three stages in the process. Two hyphæ which lie near one another (and which are generally obscurely differentiated into male and female) send out processes which meet tip to tip and cut off terminal and equal gametangia. The gametangia unite with one another and the product of their fusion swells into a black spiny zygospore. After a period of rest the zygospore germinates by means of a hypha, which usually gives rise at once to a terminal sporangium where the hereditary characters which make for maleness and femaleness are sorted out. Hence half the spores derived from the first sporangium will give rise to male plants and the other half to female plants. There is no alternation of generations in *Rhizopus;* the whole life history is confined to the haplophase.

II. The Sac Fungi (Ascomycetes)

126. *Aspergillus and Penicillium, the Blue Molds*

In Figs. 192, 193 we have representations of the asexual stage of two common blue molds, *Penicillium* and *Aspergillus*. They usually appear with *Rhizopus* upon bread which is well advanced in moldiness. It is evident that their spores are only tiny rounded cells which are cut off from the tips of bushy twigs which spring from the summits of their aërial hyphæ. The spores are sometimes called *conidia* (*konis* = "dust"), and the aërial hypha is the *conidiophore*. The blue

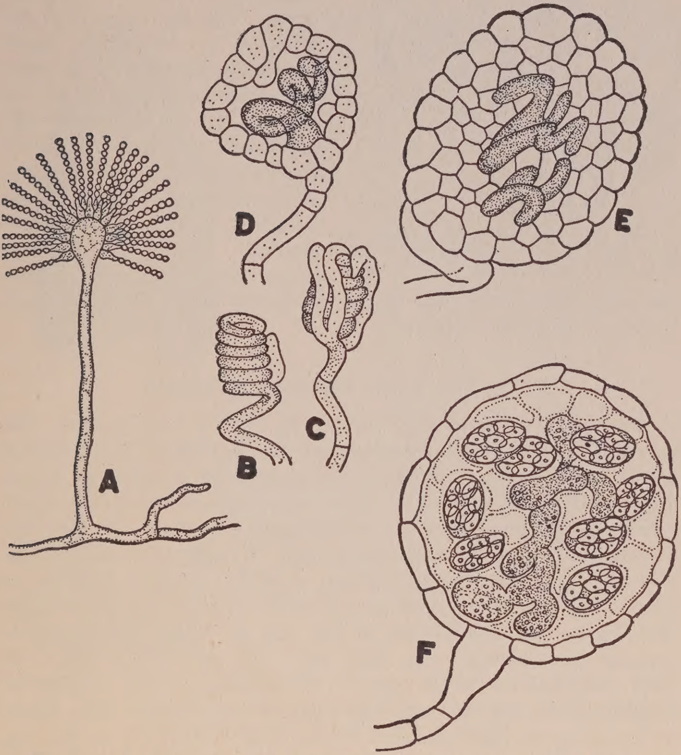

Fig. 193. — *Aspergillus:* A, conidiophore and conidia in optical section; B–E, stages in formation of sexual fruiting body; F, mature fruit (*perithecium*) containing both mature and immature asci. (B–E adapted Kny.)

molds stand in a different class from the bread-mold. Their mycelium is not cœnocytic but is divided into uninucleate cells. They carry on a sexual process, but the final result is not a single zygospore. Instead, a set of small sacs appears, inside of which the spores are borne. The sacs are called *asci* (*askos* = "a wineskin"), hence the whole class of sac fungi takes the name of *Ascomycetes*. In Fig. 193 are shown stages in the formation, and also a section of the adult fruiting body of *Aspergillus* with the eight-spored asci imbedded in its parenchymatous interior. The body itself is woven about the asci in much the same manner that the brown, protective envelope of *Coleochæte* is formed about the oöspore.

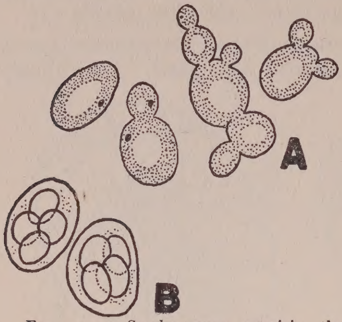

Fig. 194. — *Saccharomyces cerevisiæ*, the Beer-yeast: A, plants increasing by budding; B, two asci with ascospores.

127. *The Yeasts* (*Saccharomycetaceæ*)

The yeasts are also members of the class of ascomycetes. The bread-yeast (*Saccharomyces minor*) and the beer-yeast (*Saccharomyces cerevisiæ*) have been in use since the days of the Egyptians. In addition to these "tame yeasts" there are numerous wild species which occur on the skins of fruits and in the sugary excretions of flowers, etc. The typical yeasts are very simple fungi. If we examine microscopically a drop of a culture of molasses water into which a fragment of a yeast-cake has been stirred some hours previously, it is found full of little bodies like those shown in Fig. 194, A. These tiny plants reproduce by budding; viz., they send out protrusions which are finally detached and which continue the budding process. Sometimes fragile colonies are built up before the buds fall away. The reason for including the yeast-plants in the sac fungi is indicated by Fig. 194, B. The whole cell becomes converted into an ascus and inside it from two to eight ascospores are formed.

The well-known rôle of yeasts in the process of fermentation hardly needs discussion. They secrete an enzyme (*en* = "in" + *zumon* = "yeast") which converts sucrose into carbon dioxide and alcohol.

128. *The Higher Ascomycetes and the Lichens*

The class *Ascomycetes* includes in all some 15,000 species. Here stand the powdery mildews of which one member (*Microsphæra alni*) is responsible for the mildew which covers the leaves of lilac bushes in autumn. Here also are found the dread chestnut blight (*Endothia parasitica*), the apple scab (*Venturia inæqualis*), and the rot (*Sclerotinia fructigena*) which attacks plums and peaches.

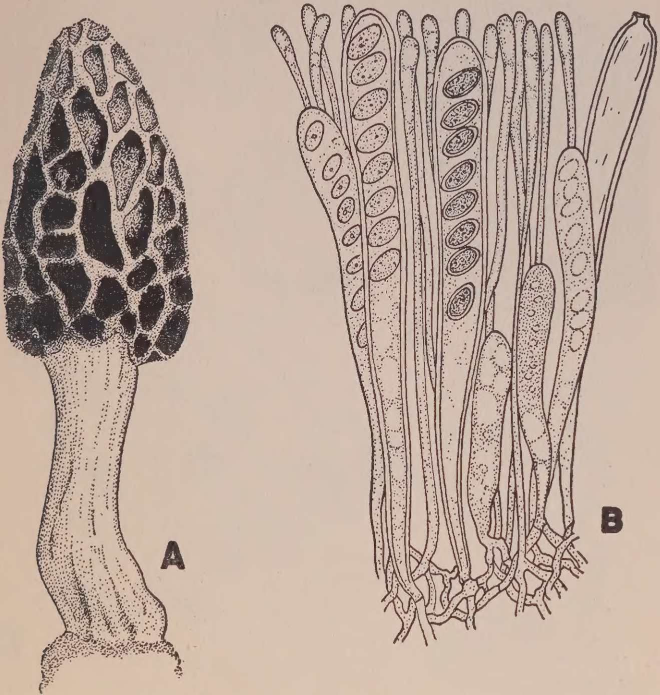

FIG. 195. — *Morchella esculenta,* One of the Fleshy *Ascomycetes:* A, fruiting body; B, cluster of asci intermixed with paraphyses.

The higher ascomycetes build up large fleshy fruiting bodies which recall those of the mushrooms. A species which possesses considerable economic importance is the edible morel (*Morchella esculenta*), which is shown in Fig. 195. The pits strewn over the conical cap are lined with myriads of eight-spored asci such as those which are shown in the figure.

A. THE LICHENS

It seems well at this point to speak briefly of the lichens. Now a lichen has no real place in any natural plant classification, since, instead of being a single plant, it is a symbiotic association of a fungus with an alga. Some 4,000 species of lichens have been described, and they assume a considerable diversity of forms. In Fig. 196 are represented a few common species. They are often found clinging to the bark of trees or to stones, and they play a prominent part in ecology, since their secretions etch and dissolve the hard rock minerals, and

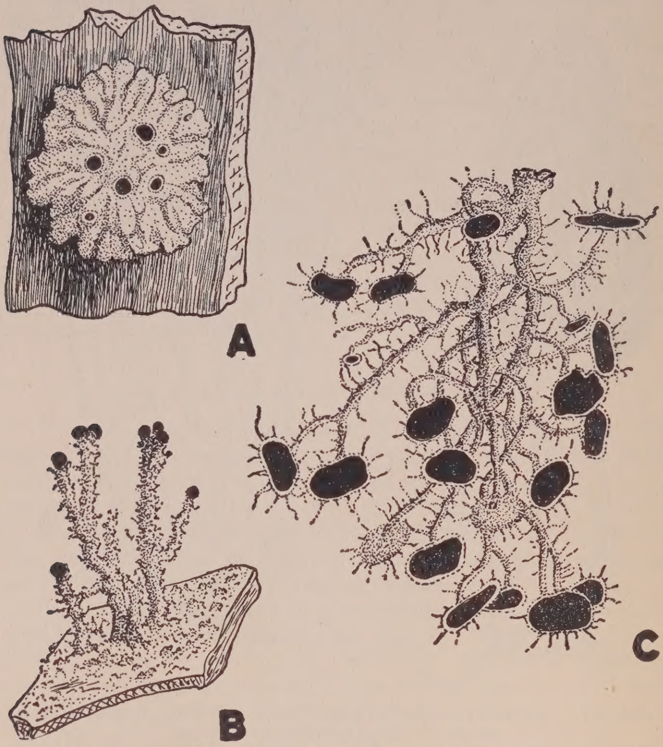

FIG. 196. — Representative Lichens: A, *Physcia* sp., a foliose lichen on tree-bark; B, *Cladonia coccinea*, a fruticose lichen which grows on dead wood; C, *Usnea barbata*, a highly evolved fruticose lichen which hangs from the branches of trees.

their dead remains slowly build up a humus substratum in which higher plants can gain a foothold.

The fungus which enters into the association is generally one of the ascomycetes, while the alga is usually a member of the *Schizophyceæ* (blue-greens), or, more rarely, one of the greens (*Chlorophyceæ*). In Fig. 197, A, B, is shown the intimate nature of the association, and the fungus seems to be getting rather the better of the bargain. In fact

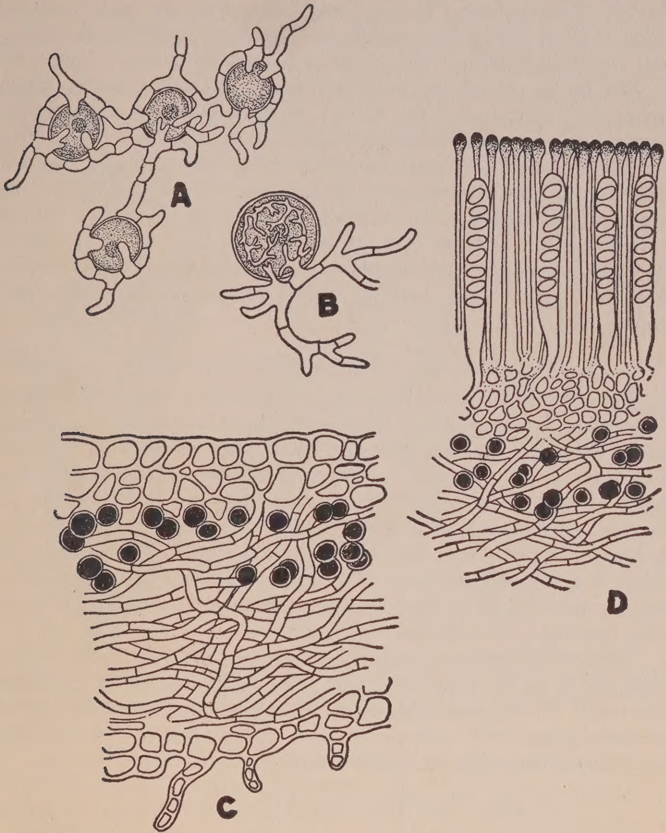

FIG. 197.—The Histology of the Lichen: A, four algal cells enwrapped with fungus hyphæ; B, the fungus has invaded the algal cell; C, cross-section of lichen thallus; D, cross-section of lichen fruiting-cup showing reproduction of the fungus symbiont by means of ascospores. (Redrawn Schneider.)

the fungus seems to have enslaved the alga in order to provide itself with carbohydrate food which the chlorophyll-bearing alga is able to synthesize. Yet the alga is given a moist atmosphere and it is also able to utilize the nitrogenous secretions and the respired carbon dioxide of its partner. In Fig. 197, C, is shown the section of the lichen thallus. Note how closely its histology resembles that of a leaf; the algal cells lie in the position of a normal palisade layer.

The lichen reproduces itself by means of small granules which break away from it and are spread by the wind; they consist of a loose tangle of fungus filaments wrapped about a few algal cells. But the fungus, when it entered into partnership with the alga, did not abandon its own reproductive devices, and it still produces little bright-colored reproductive bodies scattered over the lichen thallus. A section of one of these is shown in Fig. 193, D. The asci are elongate clavate bodies much like those of *Morchella*, and each contains eight ascospores. Long hairs known as *paraphyses* are interspersed among them.

III. The Club Fungi (Basidiomycetes)

The third great class of fungi, including about 13,000 species, takes the name of the club fungi or *Basidiomycetes*. It is so called because the spores (*basidiospores*) are borne on small, club-shaped bodies called *basidia* (*basis* = "step" or "pedestal"), and are often clustered in a group of four at its apex. The typical basidium is represented in Fig. 202. Like the asci with their ascospores, the basidium and basidiospores are the outcome of a sexual process which involves fusion of nulcei in the hyphal threads. The sexual activities of all the higher fungi, however, seem to have undergone great reduction, and they are often interpretable with great difficulty.

The basidia-bearing fungi include three distinct sub-classes known respectively as the smut fungi, the rust fungi and the mushrooms. The smuts (*Ustilaginales*) are responsible for several plant diseases of economic importance such as the smut of corn, due to *Ustilago Zeæ*, and that of wheat, due to *Tilletia tritici*.

129. *The Corn Smut* (*Ustilago Zeæ*)

The life history of the corn smut is briefly as follows. The first appearance of the disease is in the form of repulsive gray tumors which burst out on the leaves, tassels, or ears (Fig. 198, A). Examination of the malformed tissue shows an abundant mycelium running among the cells. As the tumors mature they become filled with a mass of dusty black spores which result from the conversion of the mycelium into spore powder (Fig. 198, B). The coverings of the tumors become shredded, and the spores are shed broadcast. They lie in the soil till the following spring. After the winter freezing they are ready to germinate when the snow melts. Each spore sends forth a delicate, cross-septated tube of limited growth, and from its constituent cells tiny, colorless, ellipsoid spores are budded off (Fig. 198, C). It is these spores which reinfect the corn plants by sending hyphæ into them. The tube which puts forth from the black smut spore is generally regarded as a kind of primitive basidium, and the little colorless spores which bring about the reinfection of the corn are called *basidiospores*.

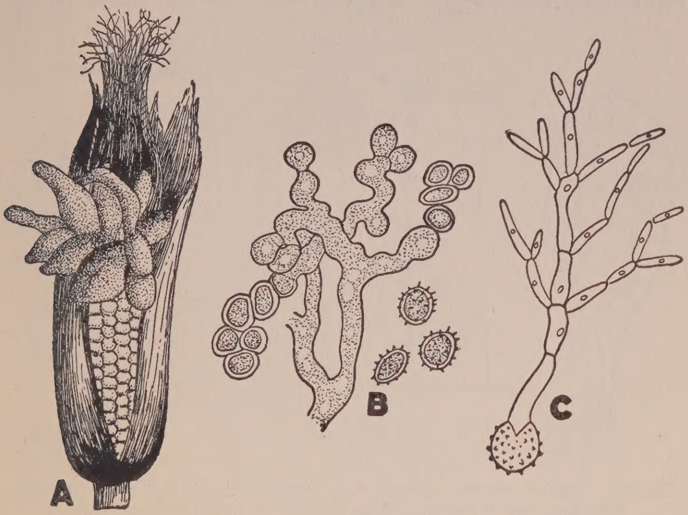

FIG. 198. — *Ustilago Zeæ*, the Corn Smut: A, ear of corn covered with tumors produced by the smut; B, group of hyphæ segmenting into smut spores; C, smut spore producing a mycelium which is called a *hemibasidium*. (Redrawn Brefeld, etc.)

The rust fungi (*Uredinales*), which constitute the second sub-class of *Basidiomycetes*, are also responsible for several serious diseases of economic plants. They take their name from the reddish color of certain of their spore masses.

130. *The Wheat Rust* (*Puccinia graminis*)

As a representative of this group of fungi we may choose the wheat rust, *Puccinia graminis*. Its life history is a curious one, involving, typically, not only the wheat plant but also the barberry bush (*Berberis vulgaris*).

In springtime one sometimes finds the leaves of barberry bushes spotted with orange-colored blotches (Fig. 199, A). Superficial examination with the lens shows that the leaf tissue at the blotched areas is thickened and that the patch is beset beneath with few to many tiny pits, often fringed around their mouths, and resembling miniature volcanoes. These constitute the *æcidial cups* or *cluster-cups*, and within them are formed millions of yellowish *æcidiospores*. It has been estimated that a barberry bush with 200 infected leaves might produce a billion æcidiospores. In Fig. 199, B, is shown a section of the æcidial cup with the æcidiospores. It will be noted also that just above the cup, with its mouth opening on the upper leaf surface, is imbedded another and smaller pouch. This is the *pycnidium*. It produces myriads of extremely tiny *pycnidiospores*, which, so far as can be determined, are functionless. It is quite generally believed that the pycnidium represents a degenerate male organ.

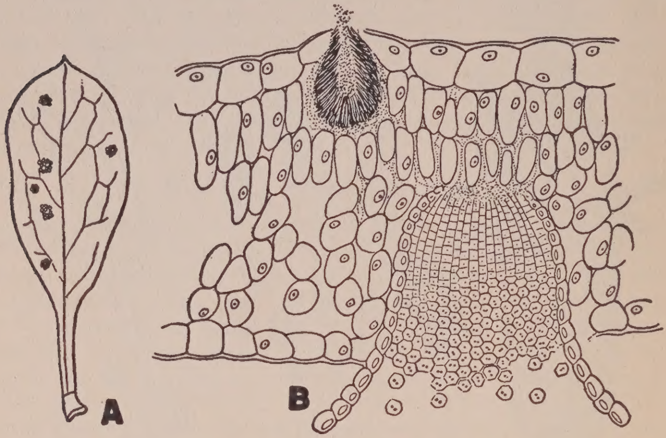

FIG. 199.— *Puccinia graminis*, the Grain Rust: A, barberry leaf bearing the æcidial cups; B, barberry leaf in section, showing æcidium below and pycnidium above.

The æcidiospores are carried by wind or insects to the wheat fields, where they bring about an infection by sending their germ tubes inward through the stomata of leaves and stems. As the summer advances, one finds that the epidermis of the wheat leaves begins to crack open in slit-like pustules which are filled with reddish spores. These are the *uredospores* and their bright color in mass is responsible for the term *grain* "*rust.*"

In Fig. 200, B, is shown a section through the uredial pustule.

As autumn comes on, the mycelium which lies beneath the uredial cluster proceeds to send up a set of bicellular spores which are deep brown or black in color and possess extremely thick walls (Fig. 200, E). These constitute the *teleutospores*, and they transform the red rust pustule into a black one. The teleutospores remain resting during the winter in the stems of the dead grasses. In the spring, with the

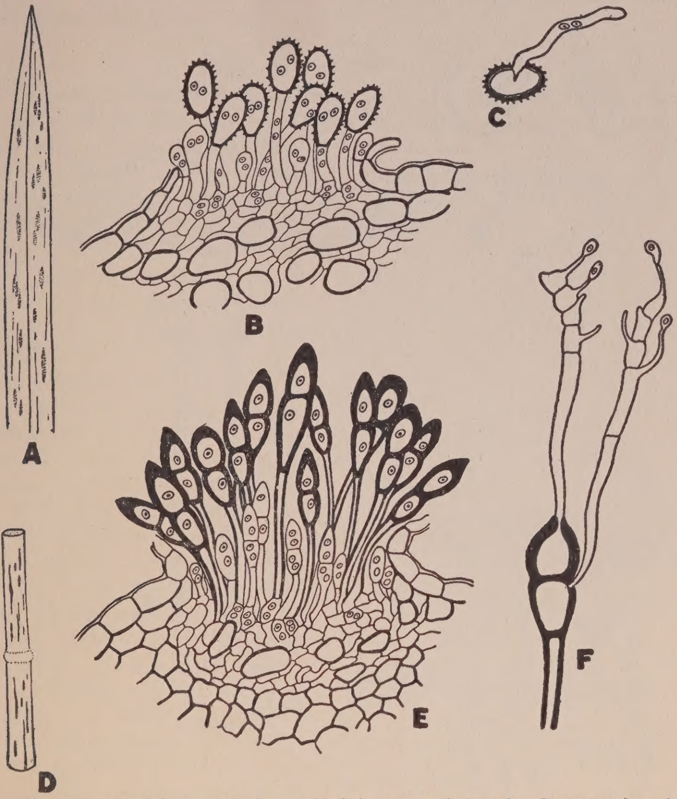

FIG. 200.—*Puccinia graminis:* A, grass blade bearing uredial patches; B, section through a uredial pustule showing both mature and immature uredospores; C, germinating uredospore; D, grass stalk bearing patches of teleutospores; E, section through a cluster of teleutospores; F, germinating teleutospore carrying two septate basidia whose sterigmata bear basidiospores. (Redrawn Gaümann [Sappin Trouffy].)

thawing of the snow and the decay of the hosts, they proceed to germinate. A germ-tube (basidium) may arise from each of the two cells (Fig. 200, F). It becomes septated into four cells, from each of which a tiny tooth, known as a *sterigma*, develops. Upon the tips of the sterigmata the colorless basidiospores arise. It is these which transfer

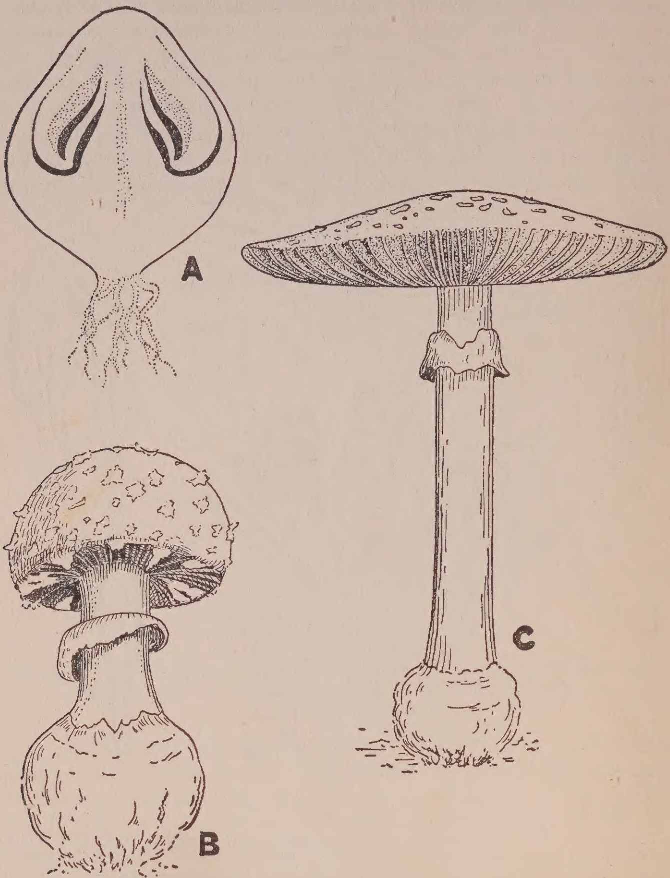

FIG. 201. — The Mushroom, Showing Stages in Formation of the Fruiting Body: A, longisection of young mushroom of *Amanita muscaria* still in the "button stage" and enclosed in a "veil"; B, elongation of stipe and rupture of the veil; C, the expanded mushroom.

back to the barberry bushes and infect the tender young leaves, thereby initiating the æcidial stage again.

Another rust which does considerable damage develops its æcidial stage on apples and hawthorns; its alternate host is the red cedar (*Juniperus virginiana*).

131. *The Mushrooms*

Highest among the *Basidiomycetes* stand the mushrooms, bracket-fungi, puffballs, etc. The true vegetative body of all these plants is a white filamentous mycelium which ramifies widely about through the substratum and is easily discovered in crumbling wood or in piles of rotting leaves. The toadstool or mushroom is only the fruiting body whose elevation into the air facilitates the dispersal of the spores. It is a remarkable structure which is formed by the weaving together of myriads of mushroom hyphæ, and its tissue, therefore, constitutes a mass of false parenchyma which is sometimes called *plectenchyma* (*plektos* = "twisted").

A typical mushroom (Fig. 201) consists of a vertical *stipe* and an expanded cap or *pileus* beset beneath with radiating plates or *gills* which are closely covered with a dense forest of basidia. A section through a single gill is shown in Fig. 202 and it makes clear the fact that the basidia are shaped like little clubs and that they bear their four spores in a terminal aggregation. This spore tetrad suggests (as is known to be the fact) that the basidium is the place where the reduction division occurs. Each cell of the mycelium of the mushroom contains two separate nuclei. It thereby exemplifies the rather rare dicaryophase condition whose position is shown on the base of the triangle of cytology (Fig. 175). Two nuclei enter each young basidium and proceed to unite. Meiosis follows promptly, and the resulting tetrad of nuclei enters the four

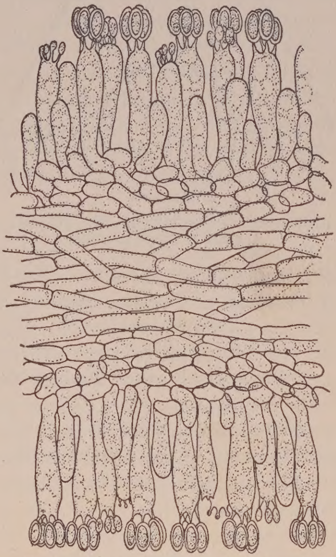

FIG. 202. — Transverse Section through the Gill of a Mushroom, Showing Central Woven Tissues and Layers of Unicellular Basidia with Sterigmata and Basidiospores.

basidiospores. The very early mycelium which arises from the spore is haplophasic, but cellular fusions among the hyphæ quickly establish the dicaryophase again. The triangle of cytology applied to the mushroom gives us Fig. 203.

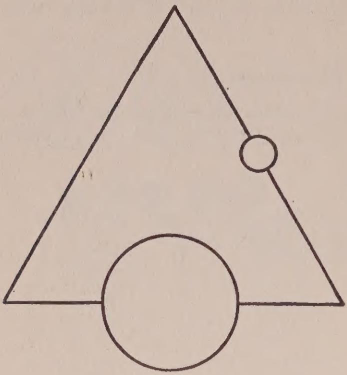

FIG. 203. — The Triangle of Cytology Applied to the Mushroom.

A few words may be added concerning the edible and the poisonous mushrooms. The layman distinguishes between the poisonous "toad-stools" and the edible "mushrooms," but the distinction is a pointless one. The only test of a newly discovered species as to its edible or poisonous quality is to try it out cautiously. If you get a stomach-ache then it would be well to avoid that particular species in the future. Actually it is very unsafe to go meddling with unknown mushrooms. The "mycophagist" should be very sure of his species. For the alkaloid poison which occurs in the deadly amanita (*Amanita phalloides*) there is no known antidote, though if the amount taken be not too large the patient may recover.

It is evident that the study of the fungi has necessitated a digression in the evolutionary story. These strange, colorless, and often degenerate plants can contribute little to the great drama which led to the establishment of the dominant flora of the earth. In the next chapter we take up once more the thread of the story of the evolution of the green plants.

CHAPTER XX

EMBRYOPHYTA (ARCHEGONIATÆ)

132. *Introduction*

We have now reached the second great sub-kingdom of plants, the *Embryophyta* or *Archegoniatæ*, which stand opposed as a natural division to the heterogeneous miscellany of plants known as *Thallophyta*. The term *Embryophyta* refers to the fact that the offspring passes its early life in association with the maternal tissues which nourish it through a definite embryological period. The alternate term (*Archegoniatæ*) for the sub-kingdom pertains to the specific type of reproductive organ (the archegonium) which characterizes all these plants.

The *Archegoniatæ* may be divided into the two divisions, *Atracheata* or *Bryophyta*, and *Tracheata*. The former includes the well-known mosses whose stems possess no true tracheids. In the *Tracheata*, on the contrary, these specialized water-conducting cells are always present.

Let us begin our study of the *Embryophyta* by considering the atracheate mosses and some of the difficult evolutionary problems which are associated with them.

We have come to one of the profound mysteries of evolutionary botany — namely, the origin of the higher land plants. We are forced by numerous lines of evidence to believe that they came up out of the water, but up to the present time the exact story of the transmigration can only be reconstructed in theory. We can trace the procession of the algæ to the very shores of the sea, so to speak, but there the line breaks to recommence with the mosses and ferns on the landward side of the divide. It is a matter which has provoked abundant and ingenious speculation.

To pass from delicate green algal plants to sturdy mosses, lycopods, and ferns is no easy matter. On the one hand we have a plant buoyed up by the water, soaking in its food salts over its whole body surface, and dependent upon water for the transport of its reproductive cells. On the other we have a land plant provided with mechanical tissues which enable it to stand "on its own feet," absorbing its food salts through its base, and transporting them through its body by means of an ascending water current. Moreover the motile germ cells now find that conditions for their activities have become inconstant and precarious.

In addition to these physiological problems there is a decided botanical difficulty to be overcome. All the higher land plants exhibit heterothallic alternation of generations. Yet there is not known a single green alga which possesses this type of alternation. Indeed, alternation of generations of any sort is a very obscure phenomenon in green algæ, and since it is homothallic it has only very recently been detected by means of chromosome counts.

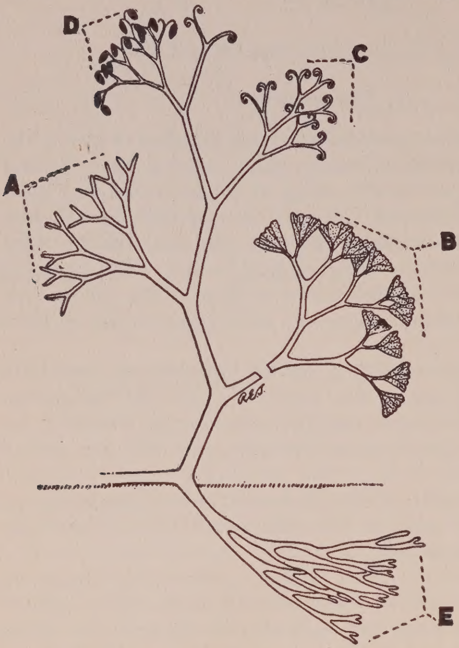

Fig. 204. — A Purely Hypothetical Primitive Land Plant Based on Lignier's Theory. Branch A is shown in its ancient algal condition; branch B has flattened out the tips of its branches to form leaflets (cf. certain ferns); branch C is like A, but in a young state with its tips coiled after the manner of many fern fronds as they unfold; branch D is shown as fertile and bearing sporangia; branch E has entered the soil and become a root.

Professor Bower has worked out in detail a theory which suggests that the algæ which effected the transition were types which possessed no alternation of generations at all, and that a sporophyte was evolved after they reached the land. It proved to be a superior adaptation to the new conditions and forged rapidly forward till it completely dwarfed the gametophyte, finally reducing it to an insignificant few-celled body.

On the contrary, faced with the difficulty of finding any aquatic plants which might serve as ancestors to the higher land forms, a more recent theory* boldly grasps the principle of analogy and synthesizes a hypothetical race of ancestral green forms out of factors which are found to-day scattered among the green, brown, and red algæ. The race is supposed to have exhibited alternation of generations of either the homothallic or the heterothallic type. Its members were characterized by bulky, dichotomously-branched, parenchymatous bodies like those of the laminarias and fucoids, and were traversed by strands of simple conducting cells. The heterogamous gametes were carried in gametangial branches of the *Ectocarpus* type which were later transformed into the antheridium and oögonium (archegonium) of the mosses and ferns. There was a tendency to retain the egg in the oögonium, where it was sought out and fertilized by the active sperm, even as in *Coleochæte.* In consequence, the diploid sporophyte came to be developed as a generation parasitic upon the gametophyte just as is the carposporophyte of the red algæ.

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* A. H. Church, "Thalassiophyta and the Subaerial Transmigration," *Oxford Botanical Memoir*, No. 3, 1919.

Arriving on the land, this plant sunk one of its branches into the soil, developed an upright stem sympodially, and transformed other branch systems into leaves. The student will see immediately that this speculation is exactly in line with Professor Lignier's theory, which was outlined in Part I of this book. Let us examine again the figure which seeks to show the general character of this hypothetical plant (Fig. 204). The illustration is evidently intended for a sporophyte. The gametophyte may have looked the same (homothallic) or it may have been a flattened creeping body (heterothallic). Perhaps there were different races with different conditions which took part in the movement to the land.

To make the remaining and more difficult part of the theory clear, it seems better to interrupt the discussion at this point and to take it up again after discussing the mosses. We will leave the transmigrating algæ in shallow water, perhaps in the area where the splash of the waves can still reach them. They carry on either homothallic or heterothallic alternation, and they are making their first experimental adaptations to the land life.

I. The Mosses (Atracheata)

133. *The Structure and Life History of a Moss*

Leaving, therefore, the realm of speculation for a time, we turn to the mosses, which appear to be the most primitive of still existing land plants. About 5,000 species of them have been described. They carpet the forest floor; they grow on tree-trunks and wet rocks, and one genus, *Sphagnum*, the bog-moss, fills many swamps with its spongy, pale-green masses.

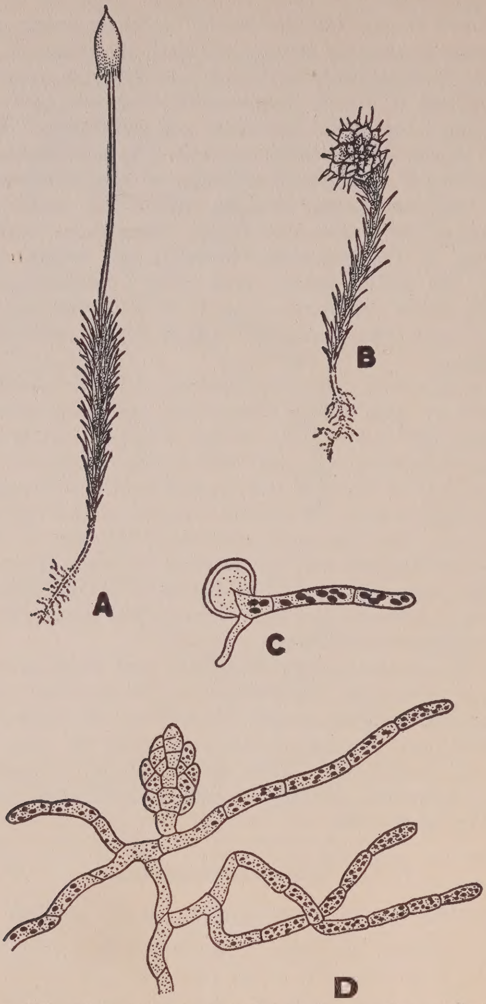

FIG. 205. — The Moss: A, female plant of *Polytrichum* bearing a stalked spore capsule; B, male plant of *Polytrichum* with antheridial rosette; C, germinating spore with protonema; D, later growth of protonemal system; certain axes have become subterranean brown rhizoids; others creep upon the surface and remain green. A bud is arising to produce the leafy stem.

A. VEGETATIVE STRUCTURES

Simple observation of a typical, fruiting moss plant shows that it consists of a basal leafy "tree" and a slender, terminal, and naked stalk at whose apex is carried a capsule filled with spores (Fig. 205, A). More careful study with the microscope reveals the fact that the leafy portion springs from a set of creeping, basal filaments which resemble the thread of a green alga. Some of them enter the soil to act as absorptive rhizoids; they then lose their chlorophyll and assume a brownish color. Tracing the life history of the plant, we will find that these threads arise directly from the spore. They constitute the *moss protonema*. After the protonema is well established one can detect small buds arising here and there from its cells (Fig. 205, D). These develop into the familiar leafy moss plants.

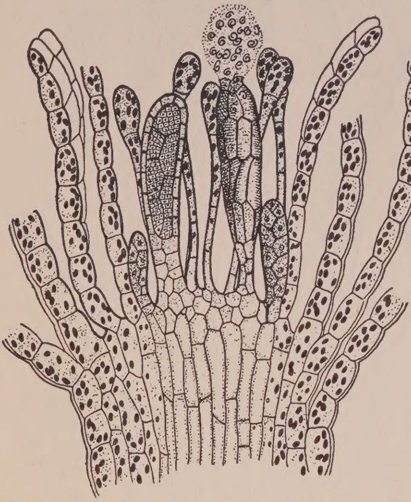

FIG. 206. — Moss Reproductive Anatomy, Male. Longisection through an antheridial rosette showing outer scales and inner antheridia interspersed with hairs. (Adapted Sachs.)

B. SEXUAL REPRODUCTIVE STRUCTURES

As the plants become mature it may be seen in some species that the terminal leaves take on a reddish color and are transformed into a small rosette which is often called the "moss-flower" (Fig. 205, B).

In thin longisection the "flower" reveals beneath the microscope the structures illustrated in Fig. 206. The stalked, many-celled, club-shaped bodies are antheridia (microgametangia), and each produces thousands of sperm cells, which at maturity are expelled from the apex of the antheridium in a milky droplet. The sperm is propelled by two cilia and it is evident that it perpetuates the ancient flagellated type of cell. So we have proved that the plant is a male gametophyte.

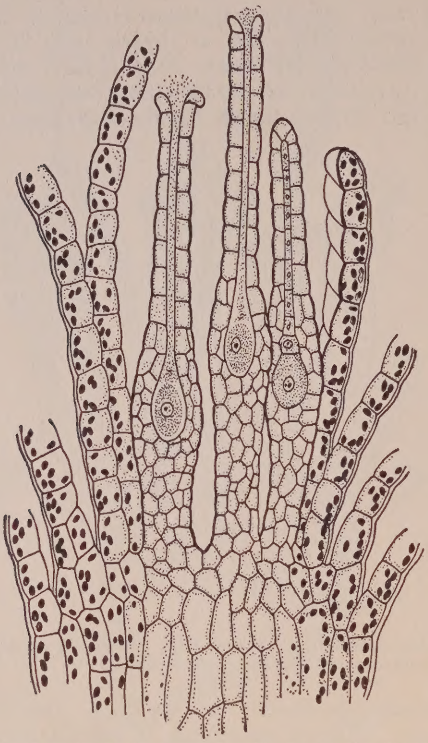

FIG. 207.— Moss Reproductive Anatomy, Female. Longisection through an archegonial rosette showing outer scales and three long-necked archegonia.

A little search reveals other colonies of moss plants whose tips form no "flowers," but which, if sectioned, reveal the appearance of Fig. 207. These are the female gametophytes, and the bodies which somewhat resemble old-fashioned lamp-chimneys are the female sex organs known as *archegonia*. They are really only multicellular

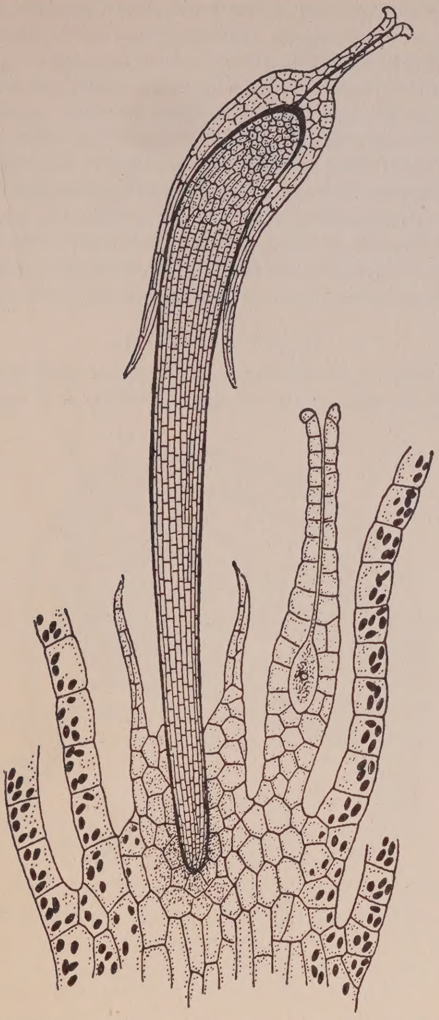

FIG. 208. — Moss Sporophyte Partly Grown. The sporophyte has sunken a foot into the tissues of the gametophyte. Its elongating stalk has ruptured the archegonium, carrying up the top as a calyptra. The capsule proper has not yet appeared. A second and sterile archegonium is shown at the right of the figure. (Redrawn Sachs.)

oögonia. The archegonium is characteristic of the whole sub-kingdom *Embryophyta* or *Archegoniatæ* with which the subsequent pages deal. It consists of a basal swollen *venter* where the single egg lies, and a long *neck* which is traversed by a fine tube called the *neck-canal*. In the young state the neck-canal is blocked by a row of cells known as the *neck-canal cells*, but these break down into thin mucilage at maturity, so that the sperm finds its passage to the egg unimpeded. The sperm is obliged to swim to the egg through the film of rain-water or dew which accumulates among the plants, though it is probable that falling rain-drops splash them about considerably. We could hardly ask for clearer evidence of the fact that the fertilization mechanism is an ancient water device which is making shift to get along on land.

C. THE SPOROPHYTE

After fertilization the egg begins to transform itself into an embryo. But just as in the case of the red alga, *Nemalion*, *it is not set free from the mother's body*. It sinks its developing base into the central tissues of the gametophyte and begins a vigorous absorption of food. The archegonium at first grows slightly to accommodate the expanding embryo, but it is soon ruptured and its terminal part is carried upward in the form of a conical cap called the *calyptra*, with which the embryo has no organic connection. The lower part of the embryo elongates into a naked stalk known as the *seta*, while its apex proceeds to build up a sporangium. This whole body, then, consisting of *foot*, seta, and sporangium, is the sporophytic or 2*n* or diplophasic genera-

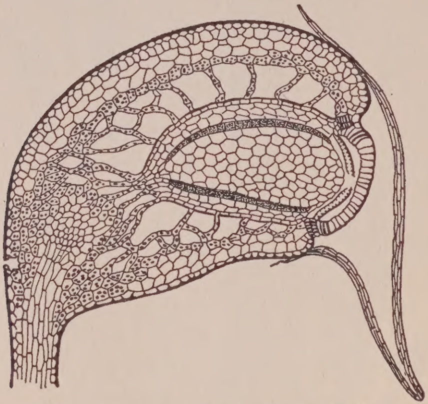

FIG. 209. — Moss Sporangium in Longisection.

tion, which grows as a parasite upon its mother's body and appears to be an organic part of it (Fig. 208).

The terminal sporangium is a complex little capsule (Fig. 209). Its wall-cells contain chlorophyll and there are even stomata at the base. Inside are found large air spaces, and through the middle runs a cylindrical *columella.* The spores arise in tetrads (which of course marks the point of chromosome reduction) and lie in a thin layer around the columella. The mouth of the young capsule is covered with a circular lid called the *operculum;* it is cast off at maturity to facilitate the escape of the spores. Around the rim of the opening a double set of hygroscopic teeth is developed which constitutes the *peristome* and by whose movements the spores are more easily freed.

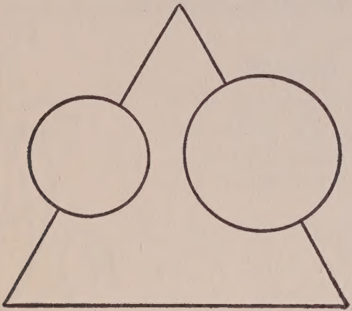

FIG. 210. — The Triangle of Cytology Applied to the Moss.

The triangle of cytology applied to the life history of the moss gives us Fig. 210. The gametophyte is the slightly larger and more conspicuous generation.

134. *The Origin of Mosses*

Let us now go back and pick up the thread of theory. We left the two generations of the transmigrating alga standing side by side in a tide-pool. Now we find one of them, the sporophyte, living as a parasite upon the gametophyte. This needs explanation.

Let us assume that the parents of the mosses shed both types of gametes freely into the water, and that fertilization took place just as it does in *Fucus* or in *Laminaria.* But when they came to the land, the menace of desiccation would be particularly threatening to the large, watery egg. Therefore it came to be retained in the oögonium (archegonium). The tiny sperm, however, could survive and move in the merest film of water. Hence it retained its ancient function of seeking out and fertilizing the egg. But since the egg was no longer expelled from the archegonium, the sporophyte was developed *in situ* and had to be nourished as a parasite by its mother. Supposing that it had once been a leafy plant like the gametophyte, its leaves now became unnecessary to its welfare, since its food, already prepared by its mother, came in through its absorptive foot. So its leaves disappeared till finally its axis alone remained in the form of a naked seta. The chloroplasts and stomata still present in the capsule wall may be regarded as lingering survivals of its ancient independent condition. Remember, this is but a theory, but as we proceed we shall find other evidence which points to its probable truth.

135. *The Liverworts*

Allied to the moss is a group of plants known as the liverworts, whose life history is identical with it. Their structure is often simpler than that of the mosses, and they are generally regarded as ancestral to them, though in accordance with the theory outlined above they may represent the outcome of a regressive line of evolution. Under this

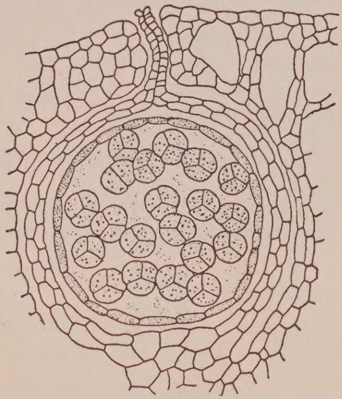

FIG. 211. — Sporophyte of *Riccia*. It is but a spherical shell containing spore tetrads. Around it appears the swollen venter of the archegonium, the neck of which still persists above.

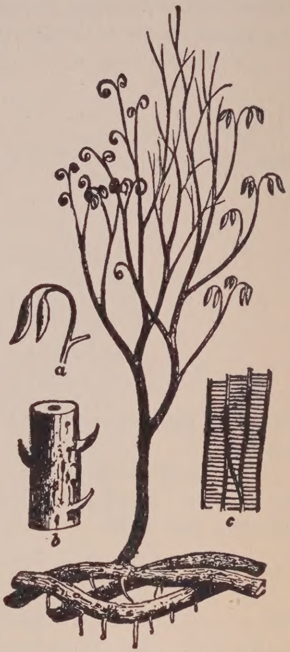

FIG. 212. — *Psilophyton princeps* (Dawson's Restoration). One side is represented as fertile; the other shows the coiled tips of the young twigs. *a*, sporangia; *b*, stems showing emergences; *c*, scalariform tracheids from the axis.

interpretation, *Riccia* (Fig. 211), whose sporophyte is a simple globe filled with spores, represents the most degenerate member. It has abolished both foot and seta and is reduced to a mere sporangium.

II. THE PSILOPHYTALES

136. *Historical and Descriptive Statement*

In 1859 Sir J. W. Dawson described and published drawings of certain peculiar plants which he had found fossilized in the Devonian rocks of the Gaspé Peninsula and which were utterly devoid of roots and leaves. From their superficial resemblance to *Psilotum*, a primitive plant still living in semi-tropical regions, he called his fossil *Psilophyton* (Fig. 212). But botanists were rather skeptical about the discovery, and little more was heard of *Psilophyton* till 1917, when certain English botanists came across a deposit of similar fossils in Devonian rocks near the town of Rhynie in Scotland. The student has already been introduced to a reconstruction of one of these plants which was named *Rhynia* (Fig. 213). In the same deposits were found the remains of a plant which was named *Hornea*, and of still another which was called *Asteroxylon* (Fig. 214). *Asteroxylon* bears myriads of moss-like leaves, and its basal branches run away into the soil in the form of root-like members. *Rhynia* and *Hornea* are both of them rootless and leafless. They are all small plants; the stems of the largest of them are not thicker than a lead-pencil.

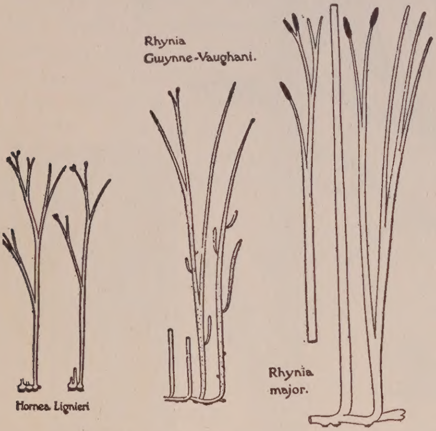

FIG. 213. — Representative *Psilophytales*. (After Kidston and Lang.)

Professor Dawson had already noted that, although the stems of *Psilophyton* were leafless, yet some of the basal parts bore prickles or emergences, not so different from the structures which are carried by the blackberries and roses. It is now suspected that these prickles are incipient leaves and that the *Asteroxylon* leaf or the moss leaf was evolved out of an emergence.

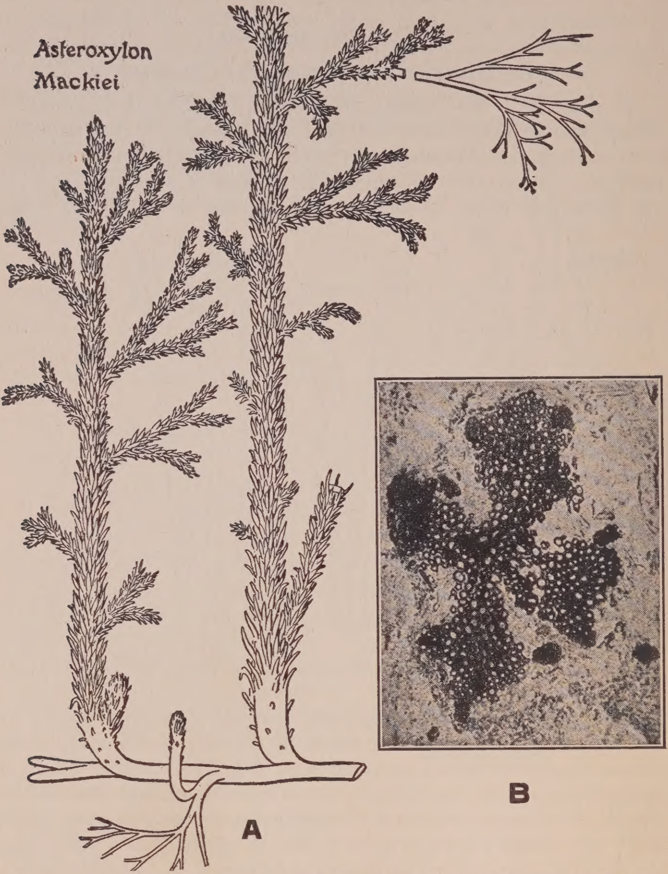

FIG. 214. — *Asteroxylon Mackiei:* A, restoration; B, transverse section of the woody axis. (After Kidston and Lang.)

But I can hear your immediate objection: "I thought you said that leaves were flattened branches!" So they probably are, generally, but it begins to look as though the tiny leaves of the mosses and the lycopods *are not homologous with the leaves of ferns and seed plants.* The leaves of the latter are possibly modified branch systems; those of the former are possibly modified emergences. It is of interest to note that Professor Lignier had already come to this opinion and had recognized a group of *Phyllodinées* whose leaves were transformations of branch systems, and one of *Phyllinées* with leaves derived otherwise. He never lived to see the discovery of the Scotch specimens which went so far toward justifying his speculations.

The stems of the *Psilophytales* are traversed by a simple stele with a solid central xylem composed of spiral or annular tracheids and surrounded by a simple parenchymatous phloëm. The xylem-strand of *Asteroxylon* is star-shaped in section (Fig. 214). The cortical layer is thick and apparently carried on the photosynthetic work.

The sporangia have been found full of spores which even show the tetrad arrangement. That of *Hornea* possesses a central columella like the moss sporangium. These plants doubtless had an alternating gametophytic generation in their life histories, but no trace of it has yet been discovered.

The *Psilophyton* plants seem to have grown in bogs. Of course we are tempted to see in them some of those much-desired "algæ of the transmigration" which had begun to transform into land plants, but the whole matter of their true affinities is highly speculative.

In this Chapter, then, we have been faced with the prospect of bridging the chasm — confessedly the most profound in the whole plant kingdom — between the aquatic algæ and the land plants. The problem is one for advanced botany, and we have barely touched upon it. The remarkable *Psilophytales* have become a focal point of interest in this connection, and research upon them is proceeding vigorously.

But, having passed this phyletic Rubicon and put the difficult mosses behind us, we see that the way forward becomes clearer. This is due largely to the fact that fossil evidence now begins to be abundant, and the actual remains of the ancestors of our still-living plants can be brought forward to substantiate the theoretical arguments.

So we will turn now to two orders of plants which ran their race in the Paleozoic Period and through the long ages since have slowly dwindled away. Once more we deal with the sweep of that same cyclic law which characterizes the destinies of all living things from microbe to macrocosm. This time we see it running in an immense arc which covers untold millions of years.

CHAPTER XXI

TRACHEATA

I. THE LYCOPODS (LYCOPODIALES) AND HORSETAILS (EQUISETALES)

137. *Lycopodium*

A. INTRODUCTION

In our open New England woodlands we find a group of evergreen plants which are generally known as club-mosses or ground-pines. Some of the trailing species are used abundantly as Christmas decorations. Most of them resemble the true mosses in form, though they sometimes attain a height of a foot or more. Others look like miniature evergreen trees with forking branches. The simpler species such as *Lycopodium lucidulum* (Fig. 215) possess no reproductive portion as distinct from the vegetative body; others, such as *L. clavatum* (Fig. 216), carry elongated yellowish cones at the tops of slender stalks upon which the leaves have been transformed into scales. The plants are often rhizomatous, and the rhizomes bear numerous forking adventitious roots.

B. STEM ANATOMY

The stem of the native lycopodium species is traversed by the type of stele which is represented in Fig. 217. It consists of bands of primary xylem made up of scalariform tracheids, between and around which lies the delicate phloëm composed of sieve-cells and parenchyma. This is a rather highly specialized stelar type, but its evolution can be traced among the species from a condition not unlike that of *Asteroxylon* (Fig. 214). It would appear that the ancestral form was a simple cylinder of primary wood, without any medulla and surrounded by phloëm. No cambium layer ever appears, and hence the adult stem can never increase in thickness; its tissues are all of primary origin. From the sides of the stele tiny leaf-traces are detached to run outward through the thick cortex to the leaves. The cortex is often strengthened with sclerenchyma as our figure shows.

C. THE CONE

The *cone* or *strobilus* is composed of flattened and imbricated scales which are called *sporophylls*, and it can easily be determined

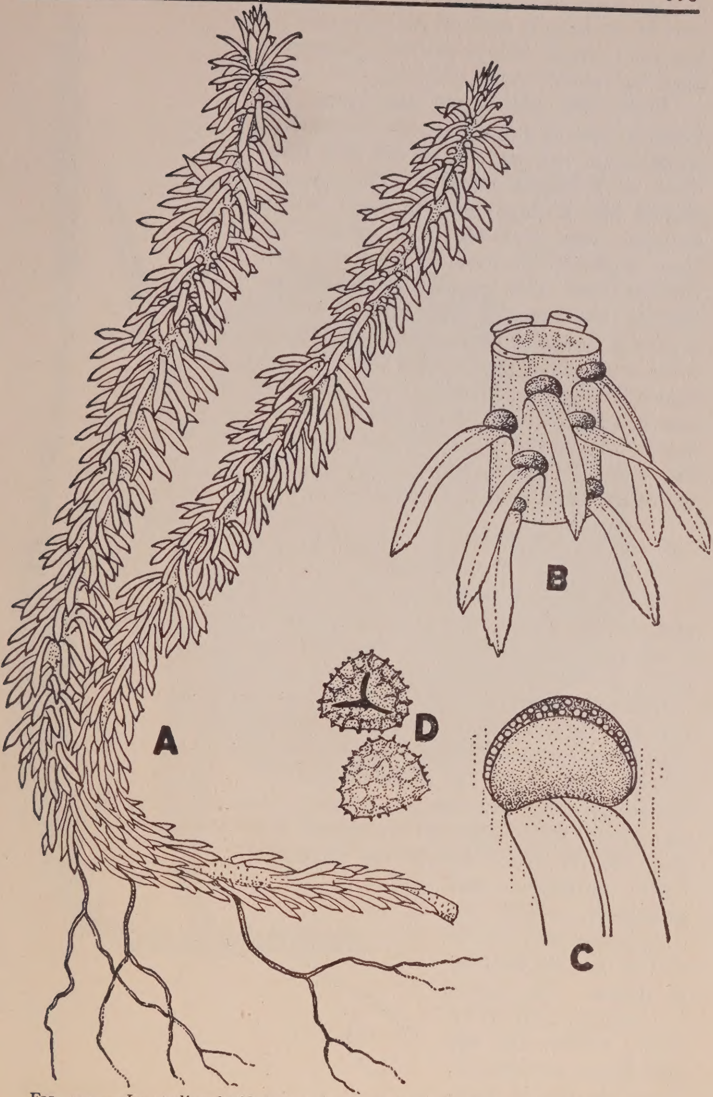

FIG. 215. — *Lycopodium lucidulum:* A, habit of the plant; B, magnified view of portion of the fertile zone; C, single sporangium in adaxial angle of its sporophyll; D, two spores.

that in the adaxial angle of each one there is located a small kidney-shaped *sporangium* filled with yellow spores (Fig. 215, C).

Under the microscope the latter are found to bear an elegant net-like sculpturing; conspicuous, too, upon each one, is a triradiate or Y-shaped marking. The spore is shaped like a three-faced pyramid with a rounded base, and the Y represents the three angles of the pyramid when it is seen from its point. This form is highly characteristic of the spores of higher plants and is always an index of former association of the spore with three sisters in a spore tetrad. Hence we may infer, right away, that the spores are the outcome of meiosis in the spore mother cells or sporocytes which filled the sporangium at an earlier stage, and that the lycopodium plant is a sporophyte.

D. THE GAMETOPHYTE AND THE ORIGIN OF THE SPOROPHYTE

The spores are distributed by the wind and are washed into the soil by rains. Here, if all goes well, the spore germinates and finally grows into the peculiar subterranean or partly subterranean body represented in Fig. 218. It is scarcely more than a parenchymatous cushion fastened to the soil by rhizoids which arise like root-hairs from its epidermal cells. Its cells are gorged with starch, and they harbor an endophytic fungus. On its upper surface are developed both antheridia and archegonia which are comparable both in form and in function to those of mosses. The sperm is a biciliate body which finally reaches the egg and effects fertilization. Then the egg is transformed into an em-

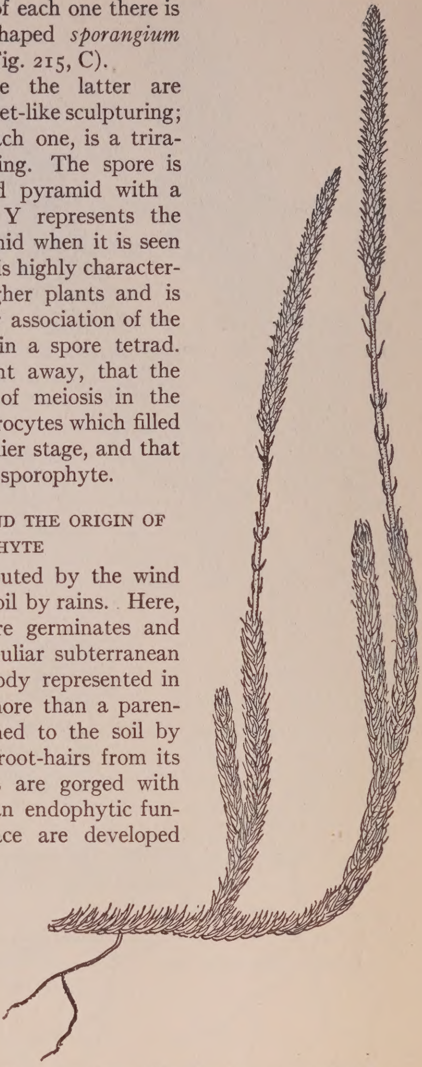

FIG. 216. — *Lycopodium clavatum*, a Lycopod with a Well-differentiated Cone.

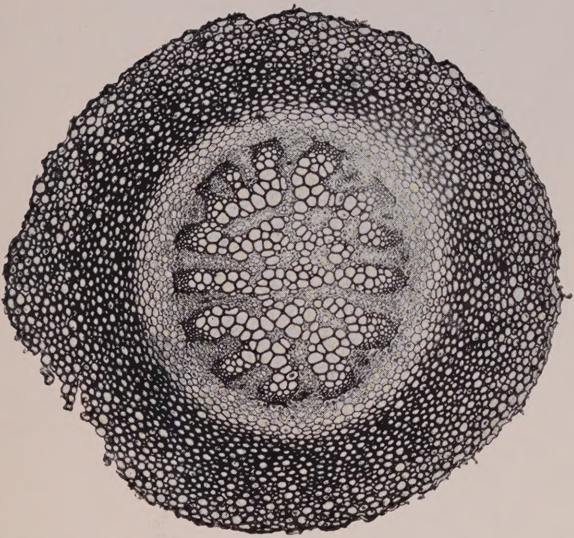

FIG. 217. — *Lycopodium clavatum*, Showing Transverse Section of the Stem. The dissected xylem is interspersed with and surrounded by phloëm, and a heavy cortex makes up the outer part of the stem. (Photograph by E. C. Jeffrey.)

bryo, and the delicate leafy sporophyte finally pushes upward into the light.

Just as is the case in the mosses, the young sporophyte is parasitic on its mother's body and absorbs its food through a foot which sinks into the maternal tissues. But as it gets older it sends out a true root of its own which pushes into the soil. Thenceforth the sporophyte lives an independent life and the gametophyte decays and disappears. *Lycopodium*, then, exhibits heterothallic alternation of generations like *Cutleria* or the moss. A word of warning, however, may avoid a difficulty into which the beginner sometimes falls in his attempt to homol-

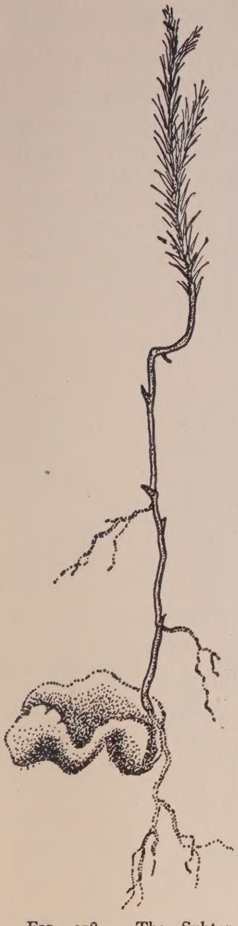

FIG. 218. — The Subterranean Gametophyte of *Lycopodium clavatum* with Young Sporophyte Which Has Arisen from an Egg.

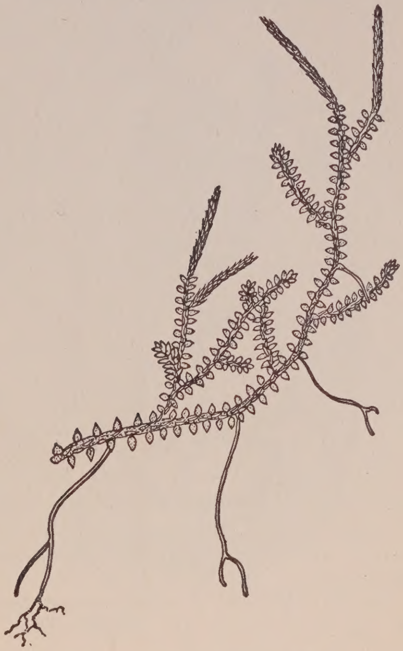

FIG. 219. — *Selaginella apus*, Showing Cones and Rhizophores.

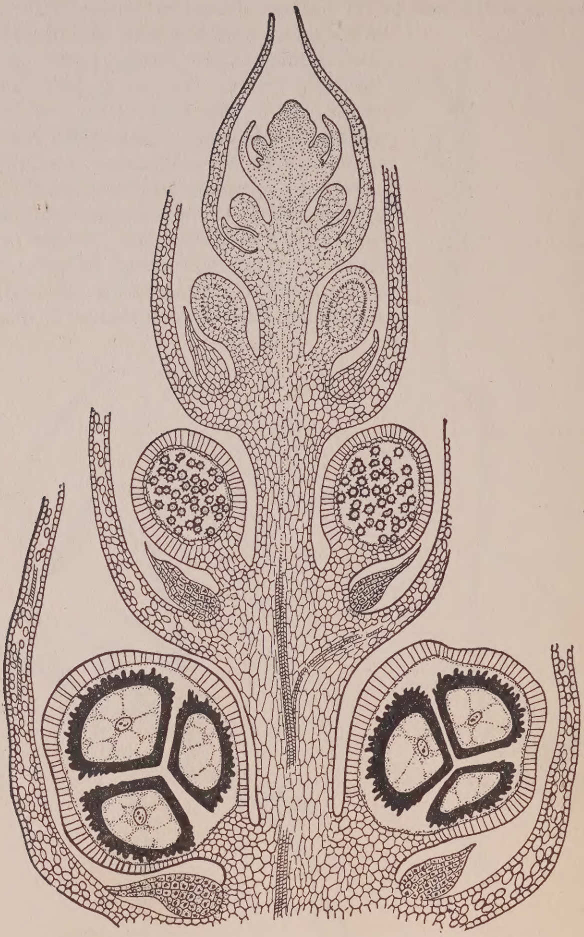

FIG. 220. — *Selaginella.* Strobilus in Longisection with Megasporangia Below and Microsporangia Above.

ogize the life histories of moss and lycopod. The *leafy* moss plant with its protonemal base is the gametophyte. The *leafy* lycopod plant, with its absorptive system composed of true roots, is the sporophyte. We must be careful not to be misled by mere similarity in external appearance.

E. COMPARISON OF SPOROPHYTES OF LYCOPOD AND MOSS

Comparing the lycopods with the mosses, we are led to wonder if the former have not perpetuated the more archaic independent condition of the sporophyte. It is not difficult to understand how the moss sporophyte might once have been a leafy plant and how it should have come to its present dependent state through a process of reduction. Finding that its mother was able to support it, it settled down to a permanent parasitism, paying the penalty in a final degeneracy which robbed it of its leaves and roots and converted it into a structure which is little more than a stalked reproductive sac.

138. *Selaginella*

A. VEGETATIVE FEATURES

We have now to consider a close relative of *Lycopodium* and one which will serve as a key to the somewhat difficult reproductive activities of the true seed plants. One species of *Selaginella* grows on moist lawns in New England as a delicate yellowish creeper among the grasses. Fig. 219 shows its general habit. It is a dorsiventral plant with unequal leaves. From its stems there push out slender, naked branches called *rhizophores*, whose tips take root in the soil.

B. HETEROSPORY

Tiny four-sided cones are carried at the tips of the branches, and it is these which demand our most careful attention. Fig. 220, representing the longisection of a cone, shows at a glance that it contains two kinds of spores and that they differ remarkably in size. Let us carefully note the terminology which applies to this condition. Whereas, the cone of *Lycopodium* is *isosporous*, that of *Selaginella* is *heterosporous*. In its upper part are found *microsporangia* filled with numerous *microspores* and standing in the adaxial angles of *microsporophylls*. Below are seen the larger *megasporangia*, bearing only a few *megaspores* (usually but a single tetrad) and standing in the adaxial angles of *megasporophylls*.

These two sorts of sporangia arise in the manner indicated by Fig. 221. At an early stage they are practically identical in histology, consisting of a mass of spore mother cells, or sporocytes, surrounded

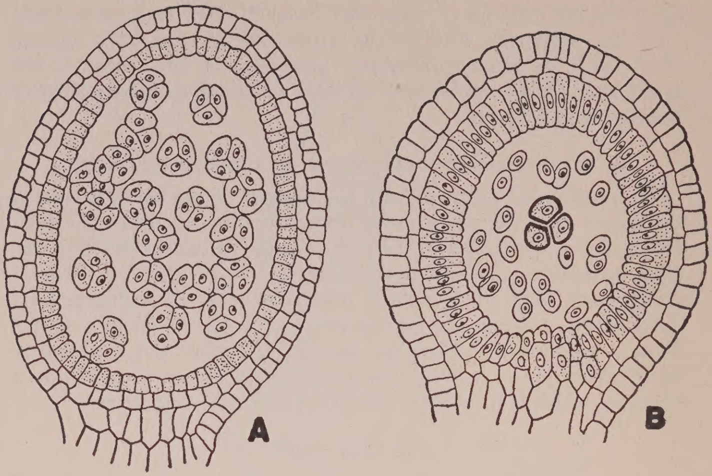

FIG. 221.—*Selaginella* microsporangium and megasporangium in the tetrad state. Only one tetrad of megaspores is arising, and the remaining megaspore mother cells are aborting. (Redrawn Miss Lyon.)

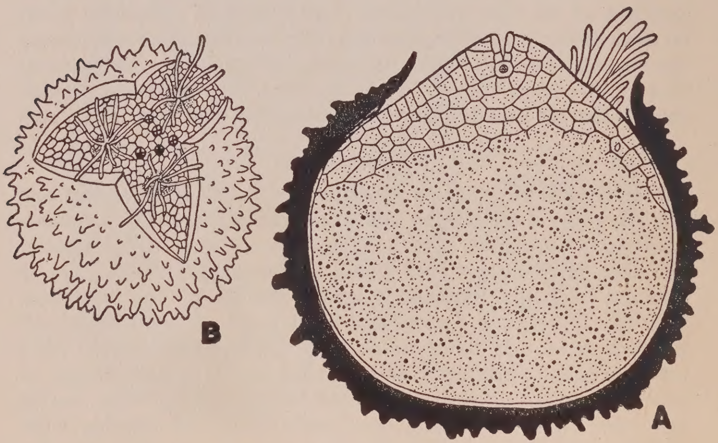

FIG. 222.—The Female Gametophyte of *Selaginella:* A, sectioned megaspore showing young female gametophyte whose cell formation is not yet completed. Later the whole cavity of the spore will be filled with tissue. An archegonium appears above and a tuft of rhizoids occurs at the right. B, perspective drawing of a megaspore split open by the expanding gametophyte. (A, redrawn Miss Lyon; B, redrawn Bruchmann.)

by a nourishing layer of cells known as the *tapetum*, and protected by several layers of wall cells. If *all* the spore mother cells undergo the reduction division, the result is a set of microspores. If, on the contrary, *only one* spore mother cell arrives at maturity, then a single tetrad receives all the available food and four megaspores appear. The meaning of the terms *microsporocyte* ("microspore mother cell") and *megasporocyte* ("megaspore mother cell"), as well as *microsporogenesis* and *megasporogenesis*, will be understood without further definition. If we will look to the etymology of scientific terms, we will rarely have difficulty with them.

C. GAMETOPHYTE DIŒCISM

So we move forward to the next step in the life history of this plant. The marked difference in the size of the spores is associated with the differentiation of the gametophytes which they respectively produce. The megaspore gives rise to a *female gametophyte*, while the microspore produces a *male gametophyte*. Here enters another striking fact. The gametophytes are not strong-growing plants living a free and independent life in the earth. In fact, they never get free from the spores at all.

The megaspore nucleus passes through numerous divisions, and finally a delicate parenchymatous tissue appears and fills the whole cavity of the megaspore. As it increases it bursts the spore coat and protrudes through the crack in the form of a small mass of green parenchym (Fig. 222). In this exposed area several archegonia appear. It is clear, then, that this parenchymatous mass is the female gametophyte.

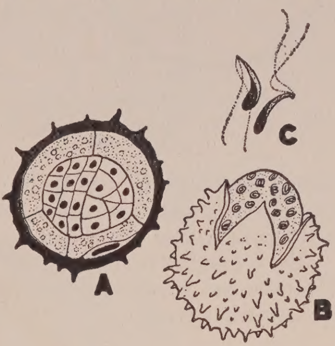

FIG. 223.—The Male Gametophyte of *Selaginella:* A, sectioned microspore showing single vegetative cell and the antheridium with spermatogenous cells; B, perspective drawing of microspore revealing protruding male gametophyte whose inner tissues have broken down to set the sperm free; C, two sperm cells. (Redrawn and adapted Miss Lyon.)

The male gametophyte develops from the microspore. It is remarkably reduced in size (Fig. 223). In fact, it produces only one vegetative cell and devotes the rest of its energies to forming a multicellular antheridium. At maturity the antheridial wall breaks down, the spore coat cracks open, and the biciliate sperm are set free, enclosed for a short time in a vesicle of mucilage. Fertilization occurs in the soil or while the spores still lie in the cone. The microspores with their sperm inside may settle down among the megaspores and the sperm may be set free into the rain-water or dew which is held in the crevices of the cone.

After fertilization the developing embryo lives for a time in parasitic fashion upon the starch-filled tissues of the female gametophyte. Then it develops its own root-system and becomes an independent sporophyte. One can now see the value to the plant of possessing a large spore filled with abundant food materials. The gametophyte cannot draw nutrient salts from the earth as it can in *Lycopodium;* its green tissues are negligible in quantity, and so upon the dominant sporophyte has devolved the work of providing food both for the coming gametophyte and for the new embryo sporophyte. The sporophyte therefore provisions the large megaspore with abundant food supplies before it is set free.

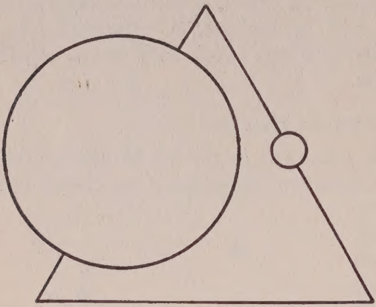

FIG. 224. — The Triangle of Cytology Applied to *Selaginella.*

The cytological triangle applied to *Selaginella* gives the Figure 224. The male and female gametophytes are represented as merged into one tiny haplophase.

D. COMPARISON OF GAMETOPHYTES OF SELAGINELLA AND MOSS

If we compare this figure with the one of the moss (Fig. 210), we are impressed with the striking difference. In the moss the gametophyte (haplophase) is the dominant generation and the sporophyte (diplophase) is relatively insignificant. In *Selaginella*, the tables have been turned completely, and the sporophyte is the dominant generation. The figure for *Lycopodium* would be about the same as that for *Selaginella*, though the right-hand circle (haplophase) would be slightly larger in proportion.

139. *The Fossil Lycopods — Lepidodendrons and Sigillarias*

The living representatives of the lycopod order are all insignificant plants like *Lycopodium* and *Selaginella.* The study of the fossil representatives, however, has revealed a most astonishing situation as regards their ancestors. Back in Devonian and Carboniferous days

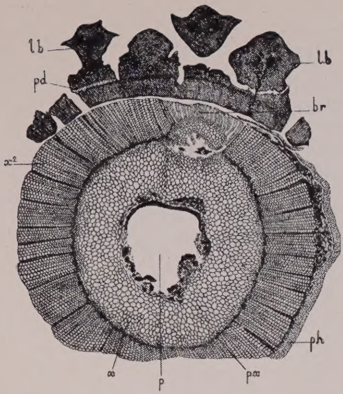

FIG. 225. — *Lepidodendron brevifolium,* Showing Transverse Section of Trunk. The pith has practically disappeared, leaving a central cavity surrounded by primary wood which in its turn is enclosed by the secondary wood. To the right are seen a fragment of the bark and leaf bases. (After Jeffrey [Scott].)

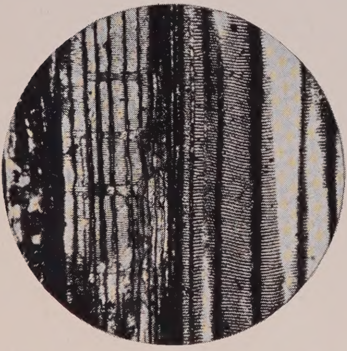

FIG. 226. — Radial Section of *Lepidodendron* Stem. At the right appear large tracheids of the primary wood; at the left, the narrower tracheids of the secondary wood traversed by wood rays. (Photograph by E. C. Jeffrey.)

they were represented by noble trees known collectively as lepidodendrons and sigillarias, which towered sometimes to a height of 150 feet and possessed trunks four feet in diameter at the base. These forest giants were anchored to the swampy soil where they grew by means of far-flung and forking rhizomes which seem to have spread outward to a distance of fifty to one hundred feet and which bore myriads of slender roots. The trunks sprayed out above into myriads of dichotomizing branches, and the younger twigs were thickly set with needle-like leaves, usually rather short, though in the exceptional cases of certain sigillarias they grew to be a yard long. When the leaves dropped from the branches they left characteristic scars, and the scarred twigs are familiar fossils in the shales of the coal-mines (Fig. 227).

From the standpoint of stem anatomy they have revealed an extremely interesting evolutionary series. The earlier forms possessed no pith and are said to be *protostelic*, but later on a pith was developed through the parenchymatization of septated tracheids just as wood parenchyma was developed many ages later, in the secondary wood of the conifers. Many of the lepidodendrons possessed a cambium layer (which is something which none of their descendants can boast) and formed a considerable thickness of secondary wood (Fig. 225), composed of scalariform tracheids (Fig. 226) and traversed by wood rays. Annual rings are lacking and this must indicate the absence of any winter season in Carboniferous time.

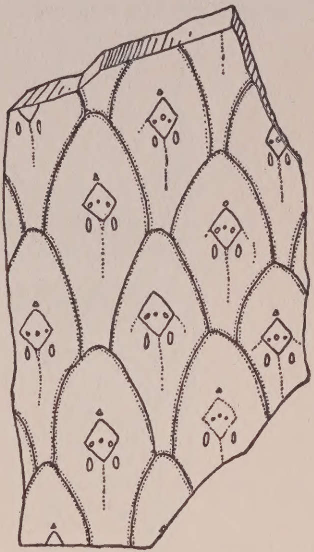

FIG. 227. — Portion of Cast of a *Lepidodendron* Trunk Showing Leaf-scars and Leaf-cushions.

The cones, sometimes a foot in length, were generally heterosporous like those of *Selaginella*, and produced megaspores and microspores (Fig. 228) in prodigious quantities.

In dealing with the structure of coal in Part II it was pointed out that the spores of ancient plants are among the prominent constituents of coal. After one has studied sections of a lepidodendron cone one can well credit the fact that a forest of trees would have shed spores enough to fill a whole swamp. The air must have been thick with dust and the earth and waters stained yellow with "sulphur," just as Kalidasa's drama *Sakuntala* speaks of

> "Rills dyed yellow with the golden dust of the lotus."

Enough is known of the spores to prove that the male and female gametophytes to which they gave rise were comparable to those of *Selaginella* and were confined to the cavities of the spores.

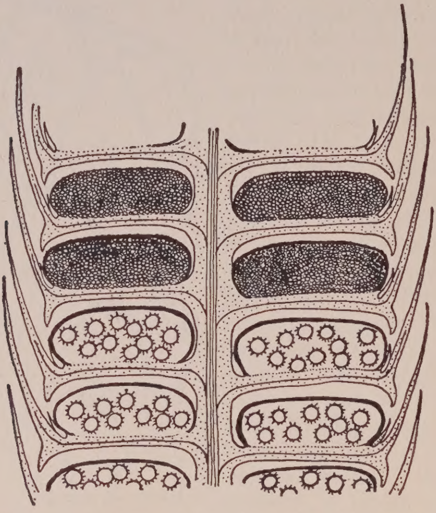

FIG. 228.—Diagrammatic Representation of a Longisection of Portion of the Heterosporous Cone of a *Lepidodendron*. These are the spores which are so abundant in coal.

140. *The Horsetails or Equisetums*

A few paragraphs may be devoted to the horsetails — a group of degenerate plants whose ancestors lived with the lepidodendrons and sigillarias in the Paleozoic swamps and grew to be leafy, reed-like plants fifty feet or more in height.

Figure 229 will identify a common species of horsetail — *Equisetum arvense*. In the spring its rhizomes send up jointed, watery-brown, fertile stems which bear cones at the top. The nodal, sheathing leaves are dry and scarious and are devoid of chlorophyll. Later in the season appear the green, diffusely branched stems. Their leaves, too, are functionless, but the green branches carry on photosynthesis.

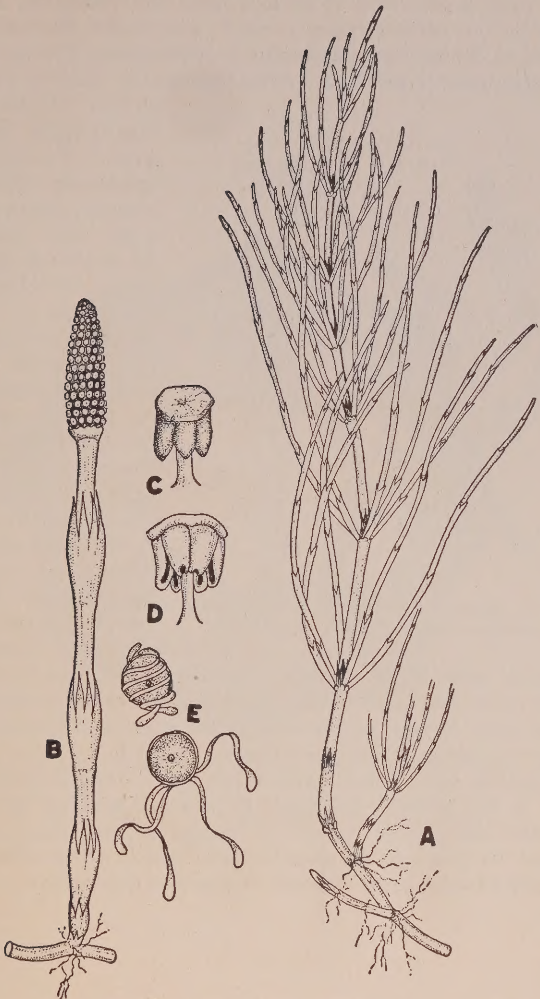

FIG. 229.—*Equisetum arvense:* A, sterile plant; B, fertile plant; C, single sporophyll viewed from above; D, single sporophyll viewed from beneath to show dehiscing sporangia; E, spores in the dry and moist states. (C, D redrawn Coulter [Wossidlo]; E, Wettstein [Dodel-Port]).

The cone is composed of an axis beset with radiating, stalked sporophylls (or *sporangiophores*) which are shaped like umbrellas (Fig. 229, C, D) and carry sporangia beneath them. The spores are all alike (*isosporous*) and bear curious hygroscopic tentacles on them so that they leave the sporangia "arm in arm." Though the spores are alike, the gametophytes (Fig. 230) are diœcious. Their form is that of a green, branching ribbon. Eggs and sperm are borne in archegonia and antheridia on the respective plants, and fertilization reëstablishes the sporophyte. The triangle of cytology would be the same as that of *Lycopodium*.

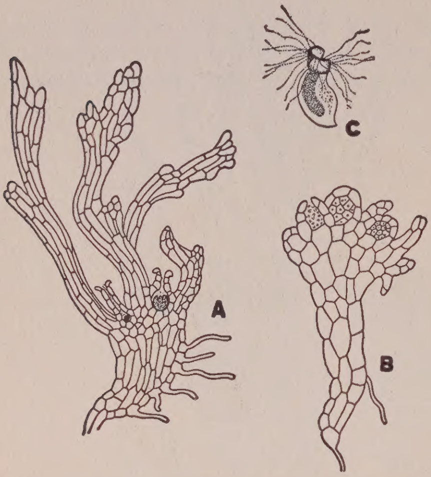

FIG. 230. — *Equisetum arvense:* A, female gametophyte; B, male gametophyte; C, a single sperm cell.

The cell walls of the stems and leaves of the horsetail are heavily impregnated with silica, and from time immemorial some of the coarser species have been used in country districts under the name of scouring rushes for cleaning floors and pots and pans. In fact, so abundant is the silica in the stems of *E. hyemale* — a species which grows in swamps and looks like a jointed green bamboo pole — that when it is burned a fragile skeleton of "glass" is left behind. The stem is traversed with an extremely degenerate siphonostele which is broken up into small strands (Fig. 231). Professor Jeffrey speaks of *Equisetum* as a degenerate herb, in contradistinction to the dynamic herbaceous angiosperms.

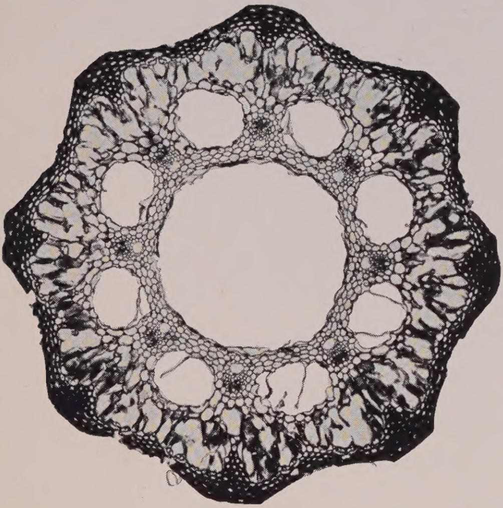

FIG. 231. — *Equisetum* sp., Showing Cross-section of the Stem. Around the pith cavity lie eight small vascular bundles each possessing a tiny canal. In the cortex occur eight large aërating vallecular canals. The stem is heavily stiffened with sclerenchyma. (Photograph by E. C. Jeffrey.)

CHAPTER XXII

TRACHEATA (*continued*)

II. THE FERNS AND GYMNOSPERMS

141. *Structure and Life History of a Fern*

The ferns as a group scarcely need to be introduced to the student, since the wild forms are familiar to every country boy and the cultivated species are well-known decorative subjects. They attain their greatest deployment in the tropics, where some grow into beautiful specimens twenty or more feet tall. Others perch themselves among the branches, or even grow attached to the bark and leaves, of trees. In our temperate woodlands we find both upright and rhizomatous species. The leaves of some, such as the Christmas fern (*Polystichum acrostichoides*) remain green over winter; others wither in the fall. The common type of leaf is the pinnately (or repeatedly pinnate) compound one, though some species bear palmate or even simple blades.

A. REPRODUCTION OF THE SPOROPHYTE

The familiar fern plant is the sporophyte, and on the under side of the fertile leaves one can easily discover the *fruit dots* or *sori* (Fig. 232). They are rather various in form and structure, but in their typical condition they are constructed upon the plan shown in Fig. 233. The sorus consists of a collection of minute stalked sporangia which radiate from a slightly elevated base and are often covered over when young by a membrane known as the *indusium*.

The fern sporangium (Fig. 234) is a small, stalked, cellular sac. A ring of specially differentiated cells with thickened walls, called the *annulus*, is usually present. Its function is to open the sporangium when the spores are ripe. The annulus is extremely sensitive to moisture, and under fluctuating atmospheric conditions it moves vigorously backwards and forwards, thereby snapping out the spores to a considerable distance. The spores are roughened, brownish bodies and are produced in the familiar tetrad condition.

B. THE GAMETOPHYTE

As they lie on the soil the exosporium cracks open and the endosporium grows outward as a small papilla. It soon becomes a septate thread whose cells are well filled with chloroplasts. From its tip is finally developed a bright-green, roughly heart-shaped gametophyte (or *prothallus*, to give it its older name), which lies flat-pressed to the earth and is attached by numerous rhizoids (Fig. 235, A). The gametophyte is a delicate body and requires a moist situation in which to live. It may attain a diameter of an inch or more. Reaching maturity it proceeds to form tiny dome-shaped antheridia (Fig. 235, D) among the rhizoids on its lower surface. Later on numerous archegonia (Fig. 235, B) appear. The fern gametophyte is, therefore, monœcious just like that of *Lycopodium*. The sperm cells are striking bodies. They are coiled like corkscrews and beset with numerous propulsive cilia (Fig. 235, E). They swim to the neck of the arche-

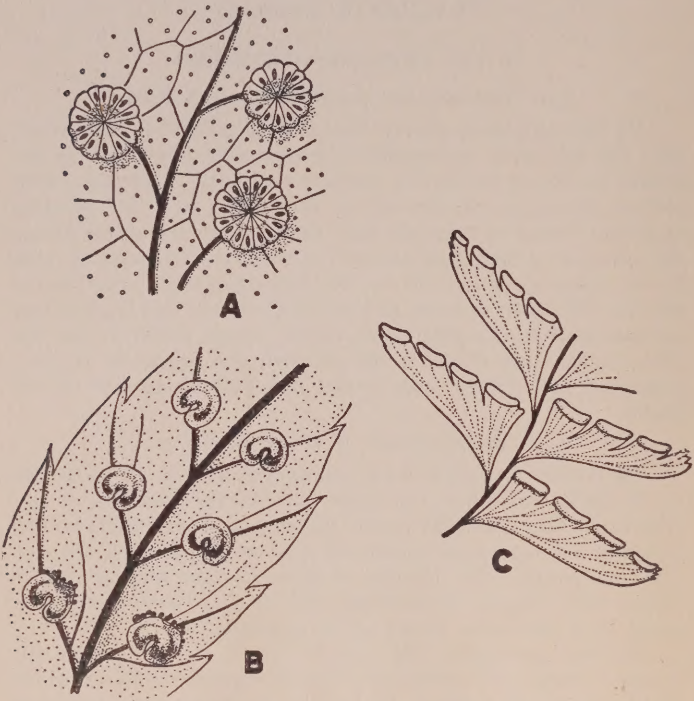

FIG. 232. — Various Types of Fern Sori: A, the simple sorus of *Kaulfussia;* B, the indusiate sorus of *Aspidium;* C, the falsely indusiate sorus of *Adiantum.*

gonium, doubtless being attracted by some chemical secretion, and enter the neck-canal in considerable numbers (Fig. 235, C). Only one fertilizes the egg. The embryo sporophyte is nourished for a time by the parent gametophyte, just as it is in *Lycopodium* and *Equisetum*. Then it sinks a root into the soil and raises its green leaves into the air and light.

The triangle of cytology applied to the ferns gives us a figure identical with that for *Lycopodium*. It is evident that up to this point in our studies it is *Selaginella* that has shown the most highly specialized reproduction. *Lycopodium*, *Equisetum*, and the fern have retained the probably older type of gametophyte which absorbs nutrient salts through its rhizoids and carries on active photosynthesis.

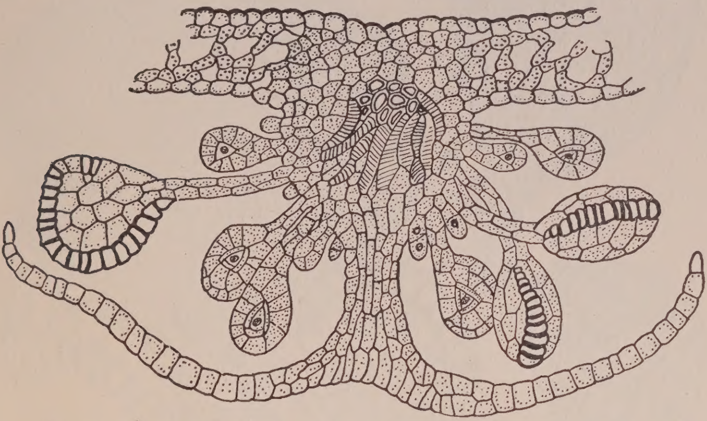

FIG. 233. — Sorus of *Aspidium* in Cross-section. Sporangia are in various stages of development. Three have developed the annulus. The sorus is covered with a peltate indusium.

C. THE FERN STELE

The vegetative anatomy of ferns almost comprises a science in itself, and the author knows of no more interesting field for evolutionary studies. There is no other order of plants which possesses such a rich variety of stelar types and offers such an amazing series of transformations through the ages.

In general it may be said that all our evidence points to the protostele as the type whence the others were evolved. It will be recalled that the stele or central cylinder of a plant is the column of tissues which is bounded outwardly by the endodermis and is enwrapped by the cortex and epidermis along with such secondary tissues (cork, cork-cambium, and phelloderm) as may have appeared.

The stele itself comprises the endodermis, pericycle (a narrow band of storage tissue just beneath the endodermis), phloëm, and xylem. Depending upon the presence or absence of a cambium layer between the phloëm and the xylem, the stele may or may not possess secondary tissues. A pith or medulla may or may not be present in the center of the stele.

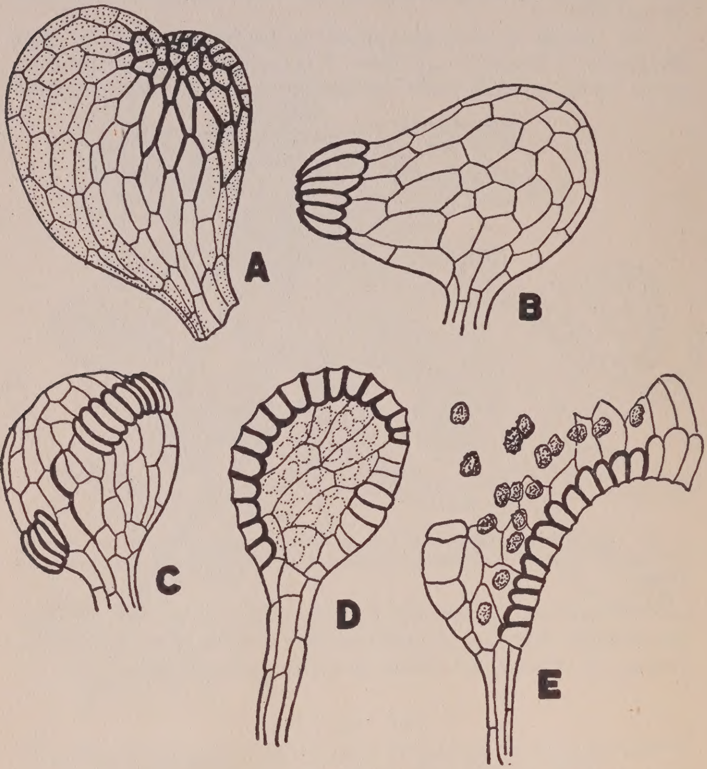

Fig. 234. — Fern Sporangia: A, the sporangium of *Todea barbara* with ill-defined annulus; B, sporagium of *Lygodium* sp. with terminal annulus; C, sporangium of *Hymenophyllum* sp. with oblique annulus; D, E, sporangia of *Pteris* in the closed and open states.

The *protostele* possesses no pith; its xylary tissues run clean to the center of the stem. In the fern protostele they may be completely tracheidal, or the tracheids may be interspersed with parenchymatous storage cells.

The evolution of a pith brings the *siphonostele* or *solenostele* into being. Sometimes one finds a phloëm layer inside as well as outside the woody cylinder; it is then called an *amphiphloic siphonostele.* The outer and inner phloëm layers under this condition are usually connected with one another at the leaf-gaps.

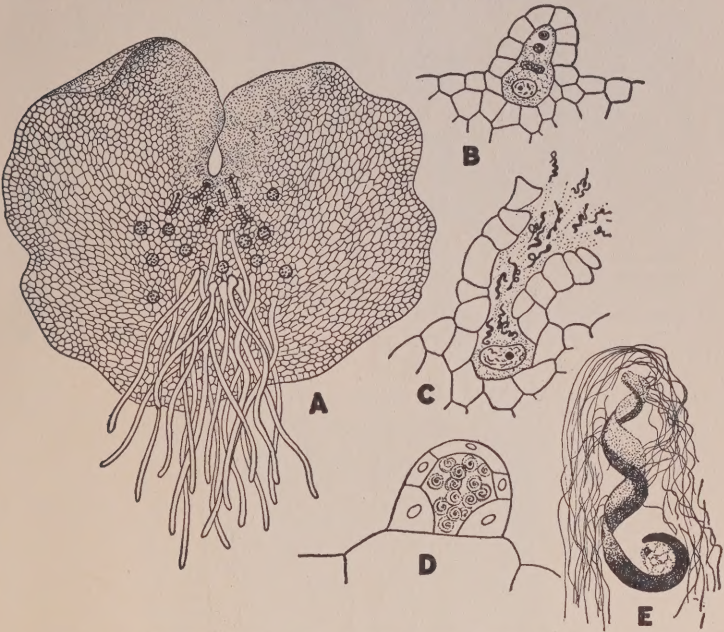

FIG. 235. — Gametophyte of a Fern: A, gametophyte as seen from lower surface; B, archegonium in young state; C, entrance of sperm into the archegonium; D, antheridium with sperm ready to be discharged; E, the fern sperm. (C, redrawn and adapted from Shaw; E, redrawn Yamanouchi.)

The more advanced stelar types are founded upon the siphonostele. Their progressive evolution involves multiplication and elongation of the leaf-gaps, perforations of the xylary tube often accompanied by complex inrollings of outer tissues, and various reduction phenomena which are often difficult to interpret upon the evolutionary basis.

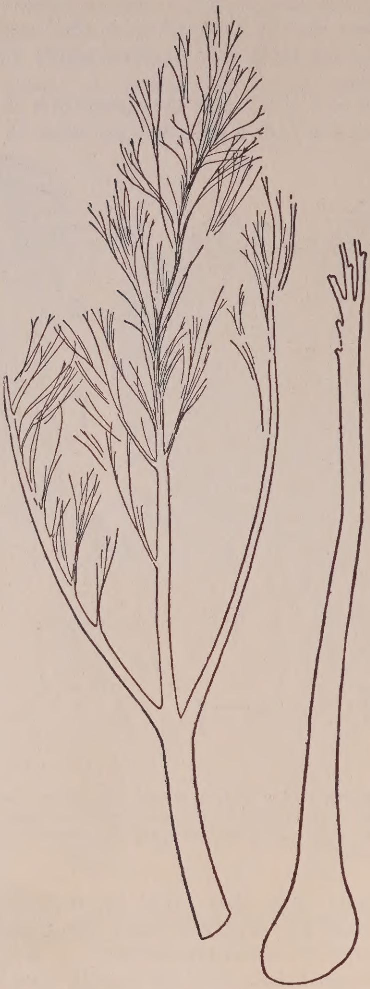

FIG. 236.—*Pseudosporochnus*, a Member of the *Psilophytales* Found in Devonian Deposits of Bohemia. Perhaps the transformation of such bodies gave the fern-frond. (Redrawn Potonié and Bernard.)

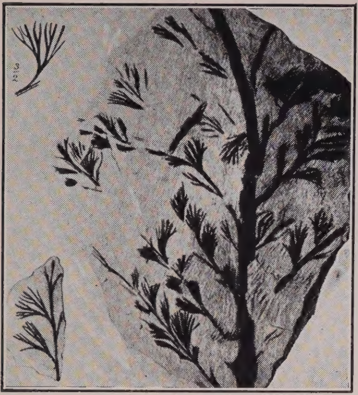

FIG. 237. — *Archæopteris fissilis*, Schmalh., from the Upper Devonian of Ellesmereland. (Natural size except enlarged detail in upper left corner. After Nathorst, 1904).

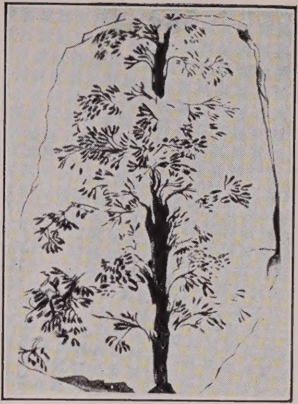

FIG. 238. — *Archæopteris Hitchcocki* (Daws.), from the Upper Devonian of United States. A fertile frond. The type specimen (natural size) after White (1905).

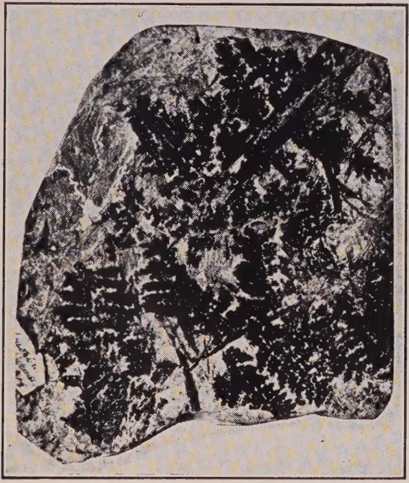

FIG. 239. — The Leaf of One of the Fossil Seed-ferns (*Lyginopteris*).

D. THE PHYLOGENY OF THE FERN LEAF

And now what can we say concerning the origin of the ferns. It has long been a difficult problem to reconcile these plants, with their large divided leaves, with the small-leaved mosses and lycopods. In recent years it begins to appear that we have found the key to the matter. The two types of leaf are probably not homologous at all. The fern leaf seems to be a modified branch system which arose after the manner of the theory put forward by Professor Lignier.*

Among the Devonian fossils allied to *Rhynia* and *Hornea* there was discovered in Bohemia the plant shown in Fig. 236, which has been called *Pseudosporochnus*. In Figs. 237 and 238 are shown two specimens of fern-fronds, one sterile and the other fertile, which come from the same ancient period of the earth's history. It seems pretty evident that the leaf of the fern is homologous with the whole bushy plant of *Pseudosporochnus*. There has always been great difficulty in distinguishing between the stems and the leaf axes of the ancient ferns, and the difficulty probably rests upon the fact that in that ancient day they were scarcely differentiated from one another.

It is evident that the fern gametophyte looks backward to the ancient water life. It is a delicate little thallus requiring plenty of moisture for its development and dependent upon water to transport its flagellated sperm cells to the archegonia.

But from now on plant life turns its back on the wet past and faces the dry future. The group of seed plants represents the successful and complete conquest of the land.

We may leave for the time the question concerning the true nature of the seed and the steps whereby it came into being, and note briefly the characters of some of the early seed plants.

142. *The Origin of the Gymnosperms*

The seed plants arose from the ferns. This concise statement rests securely upon discoveries made in the early years of the present century of certain Paleozoic plants whose leaves are indistinguishable from those of the ferns, and whose stem anatomy exhibits an interesting blend of fern and gymnosperm features. The leaves carried hundreds of small seeds with a structure not so very different from that of the pine. In Figs. 239 and 240 are shown a fossilized leaf, a sectioned stem, and one of the cupulate seeds of one of the better-known members of this extinct order of plants, which has been pertinently named the *Pteridospermæ* (*pteris* = "fern" + *sperma* = "seed").

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* Very recent discoveries of a fossil lycopod-type possessing forking leaves tends to break down this distinction and leaves the possibility open that the simple leaf is a reduction from a more complex type.

From the pteridosperms arose several orders of gymnosperms. Some became extinct in Paleozoic or Mesozoic times, but four orders survive to the present day. These embrace the cycads, the ginkgos, the conifers, and the curious, angiosperm-like *Gnetales*. Most important on all counts are the conifers, and for the present studies we will confine our attention to the pine, which is a typical member of the order *Coniferales*.

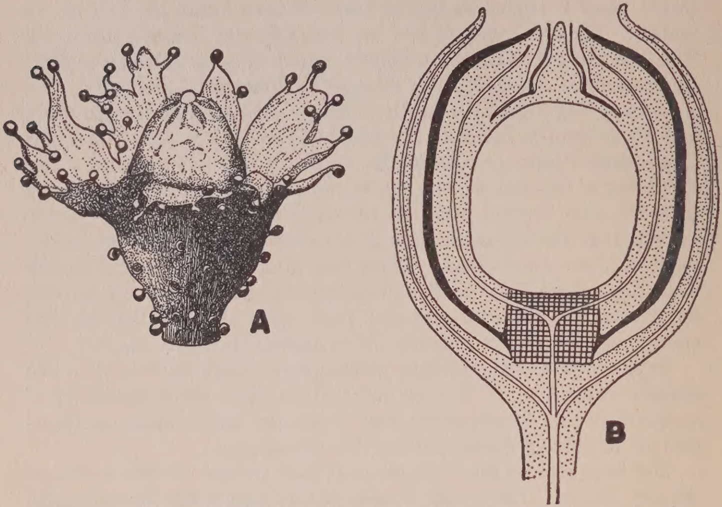

FIG. 240. — The Seed of the Plant Whose Leaf Is Figured in Fig. 239. (Redrawn Scott and Oliver.)

143. *The Life History of the Pine*

In earlier pages we have dealt pretty thoroughly with the vegetative features of the pine, and at this point we may concentrate upon the reproductive details.

A. THE MALE CONE AND MICROSPOROGENESIS

The pine is a monœcious plant. In early spring when the scaly, terminal buds of strong branches begin to unfold, one sees that clusters of male cones are appearing from some of them and solitary female cones from others. The young male cones (Fig. 241, A) are ovoid bodies beset with scores of tiny, radiating scale leaves, each of which carries two elongated sacs on its under surface (Fig. 241, B). The sacs are the microsporangia, and consequently the scales are microsporophylls. As the cone matures, each microsporangium cracks open and the powdery microspores sift out through the longitudinal fissure. They are remarkably light bodies, and their distribution by currents of air is facilitated by their possession of two bladdery wings (Fig. 241, D). The pine-tree is, therefore, an anemophilous plant.

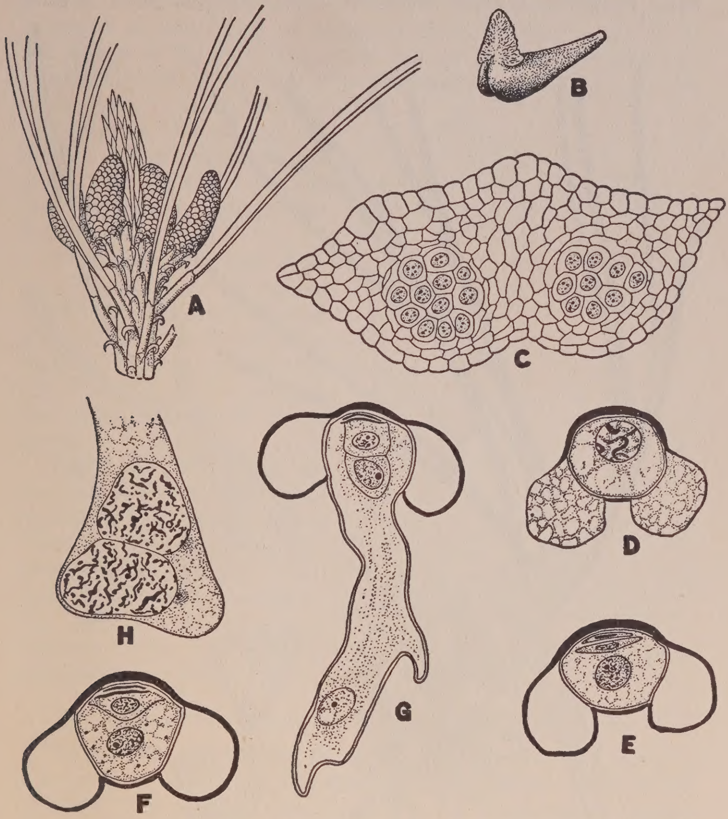

Fig. 241. — Pollen Production (Microsporogenesis) of Pine: A, cluster of male cones in early spring; B, single microsporophyll in lateral aspect; C, section through the two microsporangia of B (groups of large microspore mother cells fill the sporangia); D, a single mature winged microspore; E, microgametophyte in early condition; F, the same at a later stage; G, appearance of pollen tube (the lowermost nucleus is the tube nucleus); H, tip of pollen tube showing two sperm nuclei. (D–H redrawn Coulter and Chamberlain.)

B. THE FEMALE CONE

The female cone resembles the male in shape. Its central axis bears numerous flattened scales or megasporophylls (there is some question as to their true morphology), each of which arises from the adaxial angle of a tiny bract. In Fig. 242, C, are shown upper and lower views of the detached scales of the female cone. It is evident

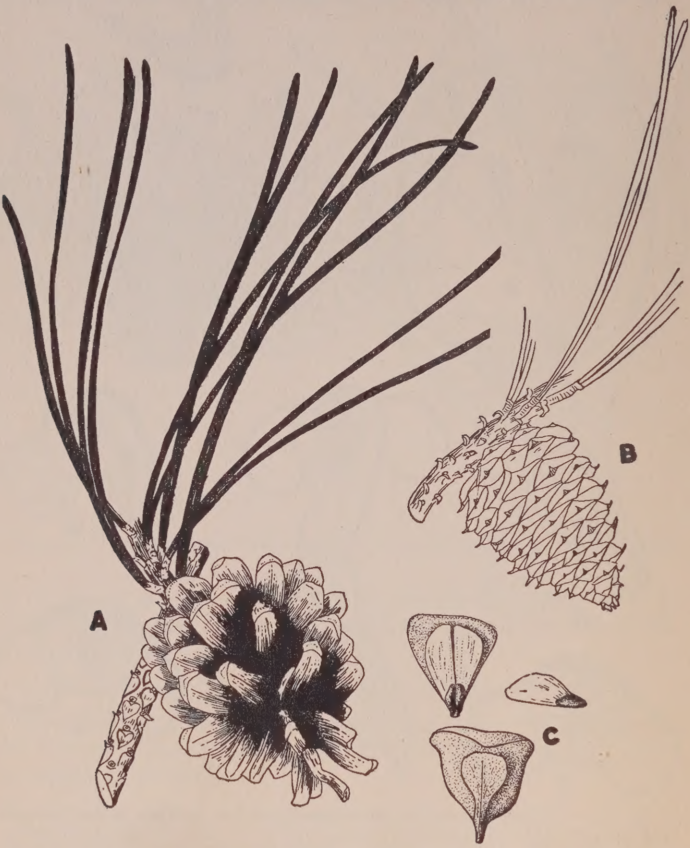

FIG. 242. — A, the opened female cone of *Pinus rigida;* B, the closed cone of the same species; C, the lower item shows the bract and ovuliferous scale of the pine as seen from beneath. The uppermost item shows the two winged seeds in position on the ovuliferous scale; at the right appears a single winged seed.

also from Fig. 244, A, that it bears two ovules whose micropyles are directed toward its base, viz., toward the central axis of the cone. It is these two ovules which are destined to ripen into winged seeds. It should be noted that the ovules lie freely exposed to the air on the surface of the ovuliferous scale and are not wrapped about by a carpellary leaf as they are in the angiosperms. This is, indeed, the feature which constitutes gymnospermy. At the time of pollination the micropyles of the ovules secrete a sticky *pollination drop* which catches the drifting pollen grains.

In the immature cone (Fig. 242, B) the scales are tightly pressed together and thereby offer protection to the developing seeds, but at maturity (Fig. 242, A) they spread apart and the winged seeds flutter to the ground.

It will be evident that we are dealing with a plant whose reproductive structures are closer to those of *Selaginella* than to those of any other plant we have hitherto studied. The microsporophylls and megasporophylls, however, have become associated into separate male and female cones.

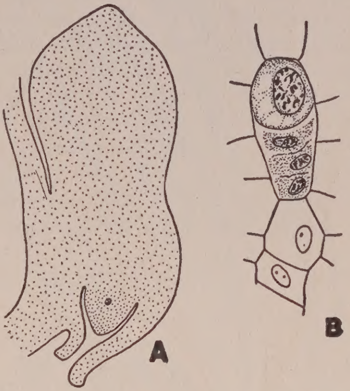

FIG. 243. — A, longisection of ovule of *Pinus* which is shown affixed to its ovuliferous scale and with micropyle directed downward; B, the linear tetrad of megaspores of the pine; only the innermost one matures into the embryo-sac of the ovule. (B, redrawn Coulter and Chamberlain.)

C. MEGASPOROGENESIS AND THE FEMALE GAMETOPHYTE

We are now prepared to go beneath the mere surface features. If we select a young ovule and section it longitudinally, we shall get the appearance shown in Fig. 243, A. In the middle rises a tongue-shaped mass of cells; this is the megasporangium or, in the older terminology, the nucellus. Rising from the base of the megasporangium in the form of a cup is the single integument which is destined to become the testa of the mature seed. Inside the nucellus lies a single megaspore mother cell, a body which is exactly equivalent to the same structure in *Selaginella*. It proceeds to undergo the tetrad reduction division, and a row of four thin-walled megaspores is established. This constitutes what is called a *linear tetrad* and it is quite characteristic of the seed plants. Reference to Fig. 243, B, shows us that the

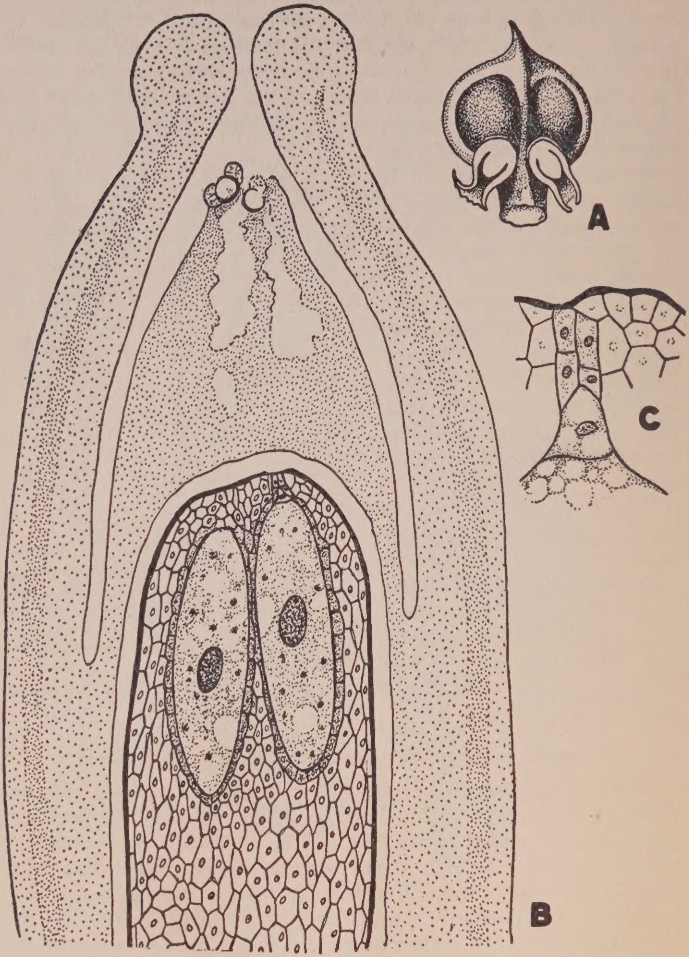

Fig. 244. — A, young ovuliferous scale of *Pinus sylvestris* with sectioned ovules in place; B, longisection of ovule of *Pinus* at the time of fertilization. The cavities in the nucellar apex were excavated by the descending pollen tubes. Two archegonia appear in the gametophytic tissue. C, apex of mature archegonium; the elongate neck is a notable feature. (A, redrawn Kerner.)

four megaspores of the pine have little resemblance to the equivalent prickly bodies of *Selaginella.* Since they are never set free from the megasporangium, a heavy, cuticularized wall is not essential to them. Only one member of the tetrad matures, and it is usually the innermost. It develops into a large cell which eventually fills the middle portion of the megasporangium.

The mature megaspore now enters upon a period of rapid multiplication of nuclei, just as it does in *Selaginella,* until some 2,000 nuclei lie inside it. Thereupon walls form between the nuclei until a mass of gametophytic tissue fills the megaspore (Fig. 244, B). At the end which is directed toward the micropyle of the ovule, two or more archegonia are developed, and although they are sunken deeply into the gametophytic tissues, they still possess the neck (Fig. 244, C) and the venter with its egg, which characterized their archaic ancestors. The egg is now ready for fertilization. But it lies deep within the megasporangium, and how is the sperm ever going to reach it?

D. THE MALE GAMETOPHYTE

Let us return to the microspores (pollen grains) which have been caught up by the sticky pollination drop which oozes from the micropyle of the ovule. As the drop dries out, the microspores are dragged inward till they rest upon the tip of the nucellus. Meantime a male gametophyte quite comparable to that of *Selaginella* has been developing inside each one of them. At maturity it consists of but six cells, of which two only are sperm cells. The number of sperm cells has been cut down remarkably. This reduction, as we shall soon see, is in consonance with the more precise method of insuring fertilization.

E. FERTILIZATION

As the pollen grain lies upon the moist surface at the tip of the nucellus, it proceeds to germinate (Fig. 241, G). Its exine cracks open, and through the cleft proceeds the intine, which bores its way downward through the tissues of the nucellus, dissolving the cells around it by means of enzymatic secretions. There is much to show that the pollen tube is really of the nature of an absorptive rhizoid which was once utilized to feed the developing male gametophyte, and that only secondarily has it been impressed into the service of fertilization. The motionless sperm cells are swept downward by the streaming motion of the cytoplasm. There are gymnosperms still in existence, such as the cycads and the ginkgos, whose ciliated sperm cells actually swim down the pollen tube — a detail which represents a most remarkable retention of the archaic fern condition. Finally the pollen tube reaches the megaspore; it pierces the membrane and discharges both sperm cells into an archegonium. One of these unites with the egg; the other perishes.

F. EMBRYOLOGY

The fertilized egg now develops into an embryo sporophyte. Some of the intermediate steps are shown in Fig. 245. A curious embryonic feature which the pine shares with many gymnosperms is an elongated, thread-like *suspensor* which forces it downward and out of the archegonium into the richly nutritive tissue of the female gametophyte. The embryo of the pine seed is polycotyledonous (though in Fig. 246 only two cotyledons are shown) — a fact which is easily proved by carefully dissecting one of the edible "pine-nuts" available in the stores. The residual, fleshy, haploid tissue of the female gametophyte is usually called endosperm, and the seed of pine may be described as endospermous.

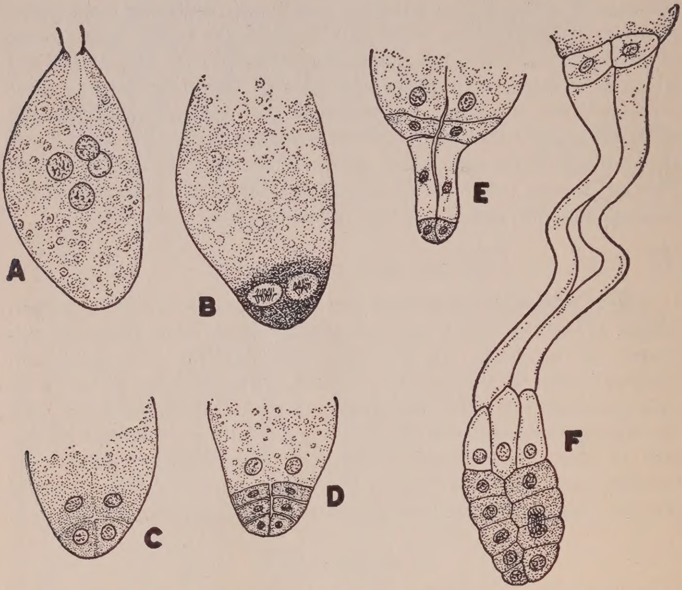

FIG. 245. — The Embryology of *Pinus:* A–D, successive stages of early embryology; E, beginning of suspensor formation; F, elongated suspensor which thrusts the embryo downward into the endosperm. (Redrawn Chamberlain.)

If the seed is planted in moist soil, the hypocotyl pushes outward and develops a primary root. After the cotyledons have digested the reserve food, they are drawn forth into the sunlight.

The maturation of the pine seed from the ovule is a slow process. In fact, three winters pass before it is mature, and in consequence one finds cones on the tree in three stages of development.

G. THE EVOLUTION OF THE SEED

From the foregoing studies the student has probably grasped the underlying nature of the seed. In fact, *Selaginella* has already supplied the key to it.

The story of its evolution from the fern sporangium runs along the following lines:

In the ancient Silurian or Devonian forests there arose a group of heterosporous ferns. The male plants bore numerous microspores in microsporangia; the females progressively reduced the spore number till only a single survivor of one megaspore tetrad remained in the megasporangium. At first both the microspores and the megaspores were shed freely from the sporangia, and as they lay on the moist soil they developed the male and female gametophytes respectively. But as the ages went by a race arose in which the sorus was reduced to one megasporangium, *which retained its single megaspore inside it.* There it developed its female gametophyte and there the egg was fertilized. For its better protection a covering (perhaps the modified indusium)

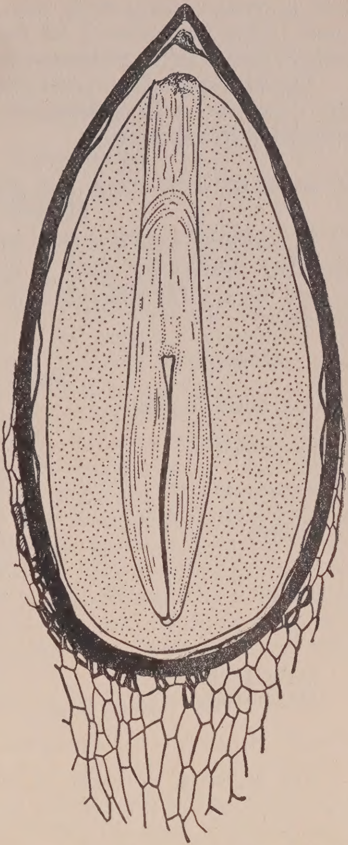

Fig. 246. — Mature Seed of *Pinus palustris* in Longisection. The black coat represents the testa. Below appears a portion of the tissue of the wing. The embryo lies imbedded in the tissue of the female gametophyte (endosperm), and the nucellus is reduced to an irregular film pressed close to the seed coat.

wrapped itself more closely about the megasporangium and became what we call the integument. The whole structure had been converted into an ovule which is really only a megasporous, monosporangiate sorus. After fertilization it fell from the parent plant, and soon its embryo pushed forth and became an independent sporophyte.

The microsporangium underwent very little change, and even today there exist certain gymnosperms in which it is hardly more than the ancient fern sporangium.

H. HOMOLOGIES OF OLDER AND NEWER TERMINOLOGIES OF REPRODUCTIVE PARTS

In earlier parts of this book we became familiar with the older botanical terminology which is applied to the reproductive parts of seed plants. The following table of synonyms should be carefully examined.

Older Term	Newer Term
	Female Parts
Open carpel (in pine)	Megasporophyll
Ovule	Integumented megasporangium
Integument	Indusium?
Nucellus	Megasporangium
Embryo-sac	Megaspore
Endosperm	Female gametophyte or haplophase
Embryo	Embryo sporophyte or diplophase
	Male Parts
Stamen	Microsporophyll — a complex of two or more microsporangia with accompanying microsporophyll tissue.
Anther locellus	Microsporangium
Anther loculus	Two united microsporangia of the typical seed plant anther — a bisporangiate synangium

The preceding discussion of pine reproduction and the above table of equivalent terms should throw a flood of light upon our previous studies of the flower. With the background which we now possess, the whole complex story of plant life is revealed as a logical evolutionary development. As we dwell upon it, always seeking to clear up the obscure points, its contemplation becomes an ever-deepening source of mental pleasure. Do you recall Huxley's words: "I cannot give you any example of a thorough æsthetic pleasure more intensely real than a pleasure of this kind — the pleasure which arises in one's mind when a whole mass of different structures run into one harmony as the expression of a central law."

CHAPTER XXIII

TRACHEATA (*continued*)

III. The Angiosperms

144. *Introduction*

So we come back for the third time to the angiosperms, but now our point of view has changed and we shall be able to see in them the culmination of the great drama of plant evolution.

In Part I our studies on the flower were dominated by ecological and taxonomic considerations; we were preparing ourselves to identify the plants of fields and woods. In Part II we studied the flower in order to familiarize ourselves with the basic principles of plant reproduction as an aspect of plant physiology. In the present study we shall be able to homologize their details of morphology and cytology with that of plants which have preceded them.

The angiosperms constitute the dominant class of seed plants, and their members all possess the closed megasporophyll (carpel) with ovules enclosed inside it. No longer are the pollen grains received directly in the micropyle of the ovule as they are in the gymnosperms. Instead, the grain comes to rest upon a differentiated portion of the carpel called the *stigma*. Here it puts forth its pollen tube, which penetrates the tissues of the style, finally enters the ovule, and effects fertilization.

145. *Fossil Angiosperms*

The phylogenesis of the angiosperms still remains an unsolved problem. The group appears in the Lower Cretaceous Period and on both sides of the Atlantic, but in genera such as *Sassafras*, *Magnolia*, *Aralia*, *Ficus*, *Cinnamomum*, *Laurus*, and others which have nothing very primitive about them. Perhaps the waters of the ocean now wash over the ancient Atlantean continent where they arose from the gymnosperms.

146. *The Caytoniales*

In 1925 there were discovered in the sea cliffs at Cayton Bay, England, and in deposits of Jurassic Age, the remains of curious plants which one must confess are actually angiospermous, though oddly enough the discovery leaves the problem of the phylogeny of

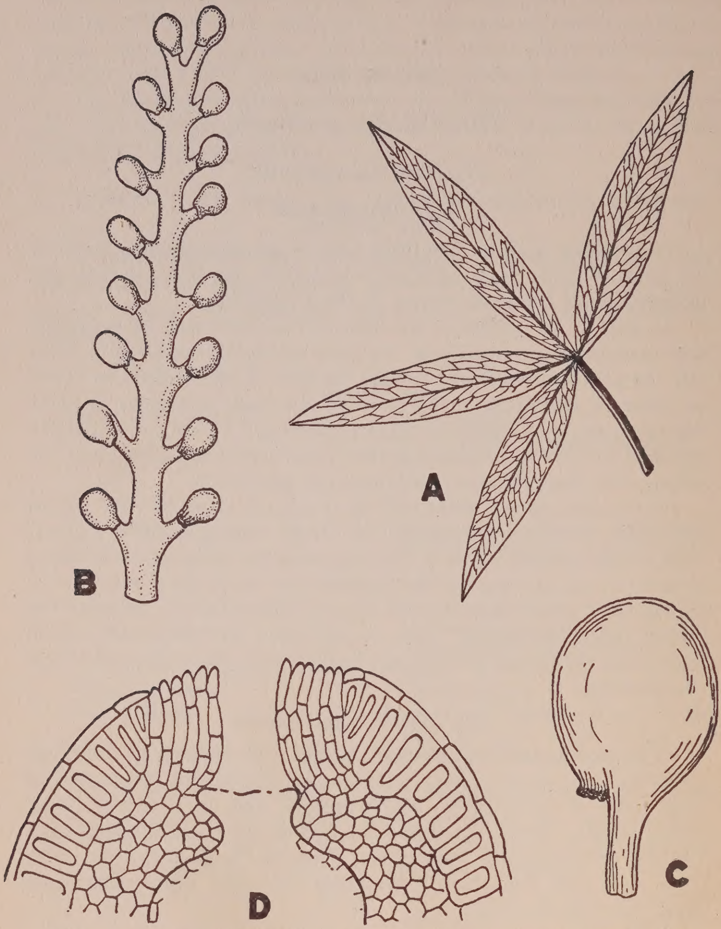

FIG. 247.—*Gristhorpia Nathorsti:* A, *Sagenopteris Phillipsi*, the probable leaf of *Gristhorpia;* B, megasporophyll with rows of seed-bearing "carpels"; C, a single "carpel" enlarged showing the basal stigma; D, longisection through the tip of an ovule taken from the "carpel."

modern angiosperms about where it was before. Two genera of these plants have been described, and reconstructions of the fragments of one of them are shown in Fig. 247. The leaf had long been known and had been classified as a fossil fern. The female reproductive parts were borne on pinnate leaves which were something like those of ferns. Each carpel seems to be a little pouch derived from the inrolling of a pinna, and over its inside are scattered numerous tiny seeds whose structure is similar to that of the gymnospermous cycads. Pollen grains are proved to have fallen upon a little stigmatic flange at the base of the pouch, and there is evidence to show that they sent pollen tubes inward to the ovules.

This type of pollen reception is an angiosperm feature. But what a peculiar position for a stigma! Moreover, botanists have always considered the angiosperm carpel to be a whole leaf folded lengthwise along the midrib. These new "carpels" seem to be derived from fern pinnæ. Actually the *Caytoniales*, in spite of their angiospermy, seem to belong in the cycad alliance — the cycads being a group of archaic gymnosperms with about nine living genera which are confined to tropical and semi-tropical regions.

So we will have to accept the fact that the modern angiosperms are without any known ancestry, and we must pass the problem onward to the next generation of botanists.

147. *The Reproduction of Angiosperms*

The details of angiosperm sporogenesis are quite similar to those of the gymnosperms. We have already described the details of microsporogenesis in Part II, largely in order to introduce at that earlier stage the phenomenon of chromosome reduction or meiosis to which it was necessary to advert repeatedly in later chapters. It will be a simple matter through comparison with the similar phenomenon in the pine (Fig. 241), to realize the significance of what is taking place.

In Fig. 248, A, is represented a section of the very young anther in which the four primordia of the microsporangia are already outlined. The dotted cells in each lobe constitute the *archesporium* from which the fertile tissue is to arise. Between the archesporial cells and the epidermis lie the *primary parietal cells*. In B, the archesporial tissue has increased in amount. In C, the microsporocytes (microspore mother cells) are mature. They are surrounded by a layer of nutritive cells which constitute the tapetum and which will break up later and send their cytoplasm in among the maturing spores. Outside the tapetum lie three layers of wall cells and the epidermis. Many angiosperms which flower early in spring pass the winter in this condition.

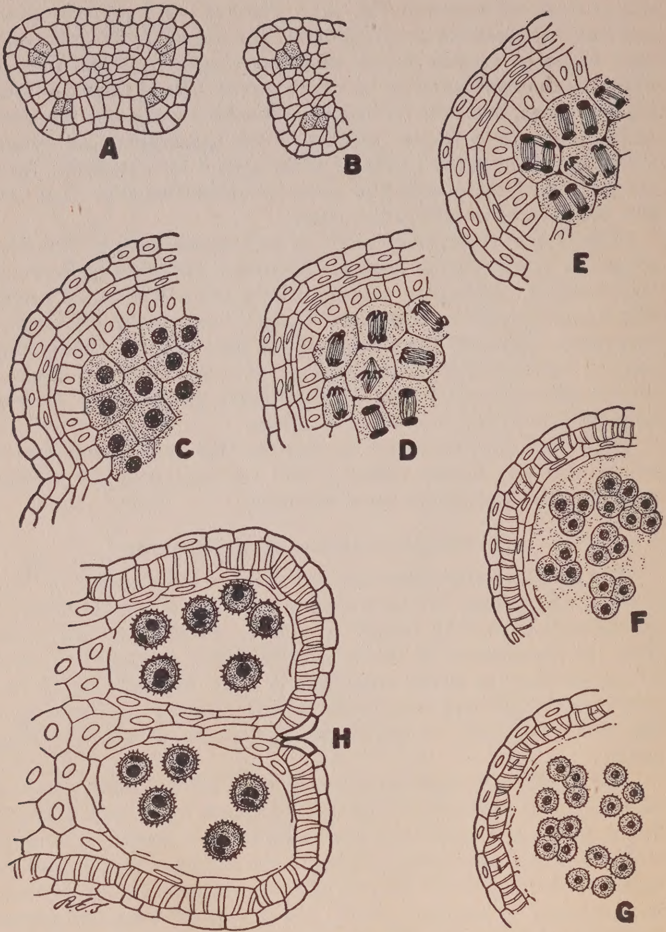
A
B
E
C
D
F
H
G
R.E.S

FIG. 248. — Microsporogenesis in the Angiosperm. Explanation in the text.

In D, E, F, and G are shown successive stages of meiosis and microspore formation. The tapetum breaks up, and it is the protoplasm derived from the disintegrating cells which lays down the spines or other ornamentations around the microspores. The outer layer of wall cells becomes modified into the *endothecium*, which constitutes an *endokinetic mechanism of dehiscence.* Finally, in H, the microsporangia are shown with several microspores in each cavity. They have already formed a two-nucleate gametophyte consisting of tube nucleus and generative nucleus. The latter is destined to give rise to two sperm nuclei. The pollen grain of *Lilium* with equivalent structures is shown in Fig. 249.

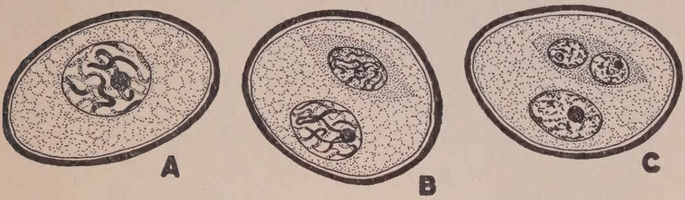

FIG. 249. — Microspores of *Lilium:* A, the uninucleate microspore; B, microspore with included male gametophyte consisting of tube nucleus (the larger) and generative cell; C, the generative nucleus has divided into two sperm nuclei. (A, B, redrawn Guignard; C, Chamberlain.)

A. MEGASPORE AND THE GAMETOPHYTES

The ovule of the angiosperm, like that of the gymnosperm, is an integumented megasporangium. Often the integuments are two, as is indicated in Fig. 251. A single linear tetrad of megaspores is formed inside the megasporangium (Fig. 250), but only one of the four comes to maturity. It constitutes the embryo-sac of the older morphology. Inside it there develops a highly reduced female gametophyte (Fig. 251). The megaspore nucleus normally divides by three successive divisions into eight free nuclei. Three of these thereupon pass to the end of the megaspore which lies farthest from the micropyle and form there three walled cells which are called the three *antipodal cells.* Three others pass to the micropylar end of the megaspore and develop there a second complex of three cells. The central member of this complex is the single egg; its fellows which stand one on either side are called the *synergids.* This group of three cells appears to represent a much reduced archegonium, and the synergids are sometimes regarded as two neck cells.

The two free nuclei which remain in the sac proceed to unite with one another to form what is known as the *primary endosperm nucleus.*

The megaspore now contains a female gametophyte (megagametophyte) consisting of six haploid cells (three antipodals, two synergids, and one egg) and one diploid nucleus.

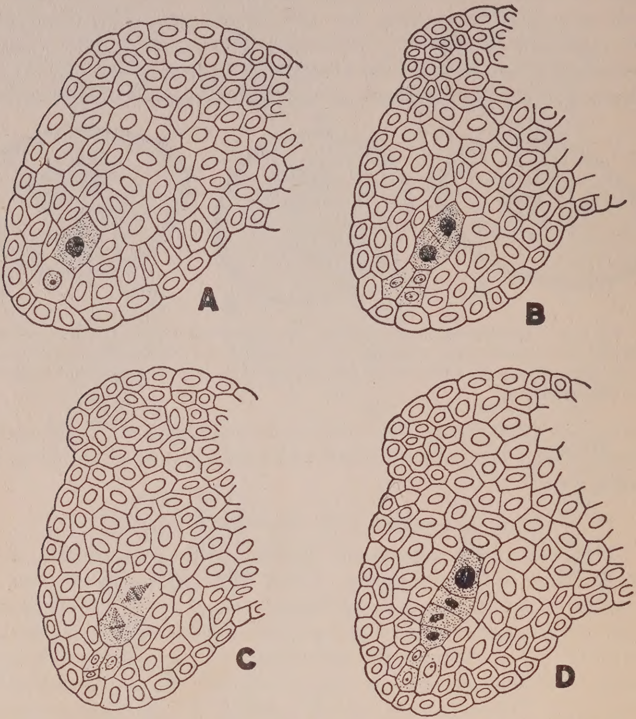

FIG. 250. — Megasporogenesis in an Angiosperm: A, the young ovule (nucellus or megasporangium) is still devoid of integuments. It contains a heavily shaded megaspore mother cell outside of which lies the more lightly shaded primary parietal cell. B, the primordium of the inner integument is appearing above. The megaspore mother cell has passed through meiosis (heterotypic mitosis), and the primary parietal cell has formed a cell group. C, the homotypic division is in progress; D, a linear tetrad of megaspores has arisen from the megaspore mother cell, but the outer three are already withering.

The mature male gametophyte or microgametophyte exhibits only three nuclei. Two of these constitute the sperm, while the third is the pollen tube nucleus.

Here, then, in these few-celled female and male gametophytes is witnessed the final reduction of the haploid generation of plants to

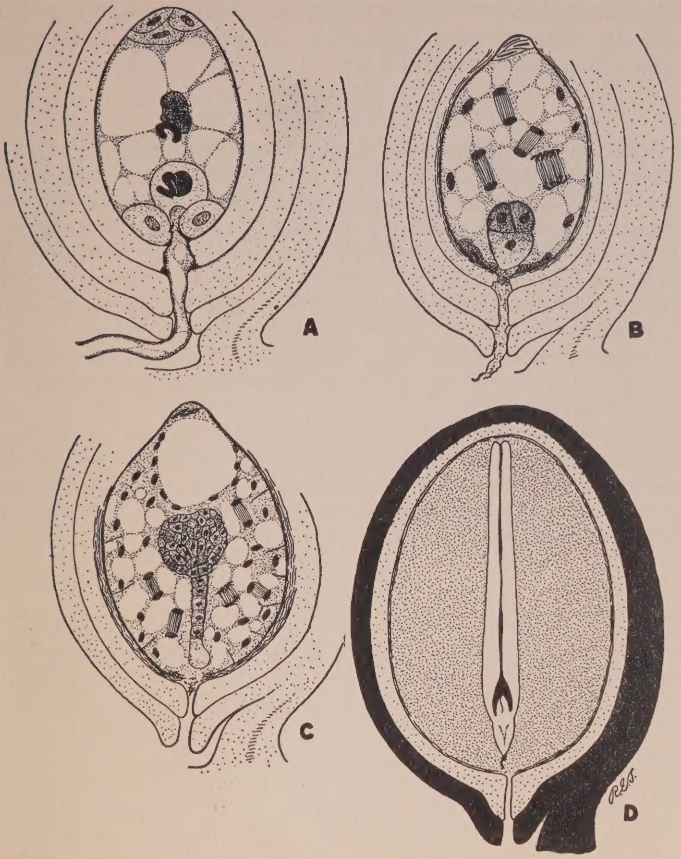

FIG. 251. — Fertilization or Zygosis in an Angiosperm and the Subsequent Embryology: A, the pollen tube has burst and expelled the two sperm, which are shown as black, coiled bodies. One of them is uniting with the egg to convert it into the zygote, while the other is fusing with the primary endosperm nucleus to convert it into the definitive endosperm nucleus. B, early embryology and endosperm formation. The egg has divided to form a three-celled embryo; the endosperm nuclei have undergone several mitoses. Synergids, antipodals and pollen tube are withering. C, later stage in embryo and endosperm formation. The embryo has differentiated a filamentous suspensor which thrusts it deeper into the endosperm. Cleavage walls are cutting into the endosperm from the megaspore membrane. The nucellus (represented by wavy lines) is being crushed by the growth of the endosperm. D, mature seed of a dicotyledonous angiosperm. Testa represented in black; tegmen lightly stippled; endosperm more heavily stippled; embryo in white. The nucellus has been crushed to a mere membrane inside the tegmen.

insignificant bodies entombed within their respective spores. It is a long step from the green autotrophic fern gametophyte to these degenerate angiosperm homologues.

B. FERTILIZATION AND EMBRYOLOGY

The sperm cells are carried passively downward through the pollen tube and are discharged into the cavity of the megaspore. One unites with the egg nucleus; the second passes onward and fuses with the primary endosperm nucleus, converting it into what is called the *definitive endosperm nucleus.* This constitutes the act of *double fertilization* (Fig. 251, A).

The egg has now become a zygote containing the diploid ($2n$) number of chromosomes. The primary endosperm nucleus, which already carried $2n$ chromosomes, has now become triploid or $3n$. The significance of this puzzling triploid fusion has never been satisfactorily explained.

The zygote now proceeds to develop the embryo sporophyte. Stages of the process are shown in Fig. 251, B, C. A suspensor of several cells is developed, and the embryo proper is transformed from a cellular ball into a dicotyledonous (or a monocotyledonous) body with accompanying hypocotyl and plumule.

C. ENDOSPERM FORMATION

The definitive endosperm nucleus has meantime entered upon an activity of rapid division which fills the cavity of the megaspore with free triploid nuclei. These are finally converted into a mass of walled cells around the embryo. This is the nutritive endosperm tissue of the endospermous seed. It is evident that it is not cytologically homologous with the tissue of the same name which occurs in the pine seed. In the latter the endosperm is the haploid gametophytic tissue which was laid down long before fertilization; in the angiosperms it is a triploid tissue of obscure significance which does not appear until fertilization is accomplished and which is, in fact, dependent upon the act.

The synergids and antipodals usually wither away; the nucellar tissue, too, is generally crushed out of existence by the enlarging endosperm and embryo. The integuments are converted into the sclerenchymatous testa and the delicate tegmen, and the ripe seed is finally set free from the fruit.

SUMMARY

In a few closing paragraphs let us try to summarize the story of plant evolution through the ages. In one sense it is a dangerous thing to attempt, since students are all too prone to take a theoretical outline for accepted fact. It must be understood clearly that there are great gaps in the history and that our endeavor to bridge them may be upset to-morrow by new discoveries in paleobotany. Nevertheless, the author believes that this attempt to get a synthetic view of the story is very much worth while. If we know definitely where we stand in a matter, it will be easier, as new knowledge accumulates, to see more clearly why and where we were at fault.

The beginning of the story of plant life is a hypothetical one. We may suggest that colonies of small "lives" of the nature of those living ultramicroscopic particles which make up the filtrable viruses gradually evolved into the visible, non-nucleated cells of the bacteria, which soon sent off the line of non-nucleated blue-green algæ.

From the bacteria perhaps the nucleated cell arose according to the principle of hierarchies which runs through the universe. This means that the nucleated cell, itself, may be a fusion product of bacterial bodies and that the nucleus was derived from the amalgamation of their chromatin content.

The early types of plant cells were chlorophyllous flagellates which sometimes bore accessory brown or red pigments and which easily became colorless saprophytes or parasites, or even developed the power to ingest solid food and to evolve into animals.

From the pigmented flagellates came the green, the brown, and even the red algæ. These constitute the chlorophyte, the phæophyte, and the rhodophyte lines of evolution. The chlorophytes experimented with moving colonies, with motionless colonies, with septated and tubular filaments. The phæophytes developed both homothallic and heterothallic alternation of generations to a remarkably high degree, till finally, among the laminarias and fucoids they almost, or even quite, abolished the haploid or gametophyte generation. It was the phæophytes, too, which rose to higher vegetative levels than did the representatives of any other algal line. They organized their cells into tissues and the tissues into cortical, phloëm, and medullary regions; their bulky bodies also learned to increase by cambial growth.

The rhodophyte line developed elaborate false tissues through the weaving together of filaments, and its alternation process rose to a high level of complexity. Since the egg is retained in the carpogonium, the carposporic generation develops as a parasite upon the gametophyte. A further complication arose through the impressing of nutritive auxiliary cells into the service of the carposporophyte, and also through introduction of the tetrasporic plant.

The fungi represent degraded parasites and saprophytes which probably descended from various classes of algæ.

The story of the early conquest of the land is an ambiguous one. It has been suggested that we may use the principle of analogy to synthesize a hypothetical race of green algæ which possessed alternation of generations, bulky bodies, tissue differentiation, and sex organs comparable to those of certain brown algæ. At the same time it showed a tendency to retain the egg in the gametangium and to develop a parasitic sporophytic (diploid) generation after the manner of the red algæ. This hypothetical race gave rise perhaps to the extinct group of plants known as *Psilophytales*. From the *Psilophytales* of the *Asteroxylon* type, with leaves derived from emergences, came the mosses and the lycopods. From those of the *Psilophyton* or *Pseudosporochnus* type the ferns arose through the conversion of branch systems into leaves. In the absence of fossil evidence all the above is little more than theory, but with the coming of the land plants hypothesis gives way to historical fact.

The lycopods ran their race in the Paleozoic Period, becoming noble forest trees with secondary tissues in their stems and with heterosporous cones. Certain species had practically reached the seed state. The gametophyte was transformed into an insignificant body which never escapes from the spore, just as we have seen to be the case in the still living but degenerate *Selaginella*. *Lycopodium* appears to perpetuate an earlier isosporous condition of the race. The horsetails, likewise, rose to their acme in the Paleozoic, and the trifling *Equisetum* is all that remains of their vanished grandeur.

The ferns developed into many orders, a number of which have persisted to the present, but their most important evolution was into the important group of seed-ferns or pteridosperms. A seed, as we should now clearly understand, is only an integumented megasporangium containing a single megaspore within which the female gametophyte is developed. From the fertilized egg arises the new sporophytic generation.

From the pteridosperms, sometimes through intermediate extinct orders, arose the gymnosperms, which have persisted into our modern world. Though their day is over, they still play a prominent part in the temperate floras of the earth. The pine serves us as a representative type of the class *Gymnospermæ*.

Finally in the Mesozoic Period, and from some at present unknown gymnospermous source, the angiosperms came into being. They constitute the dominant flora of the modern world, and, so far as we can determine, they are still forging vigorously ahead.

148. *Conclusion*

Well, "Gentle Reader," we have traveled a considerable road together, but we have come now to the parting of the ways.

What does the author particularly hope that you have gotten from these pages? Evolution! with all that the word implies. It is not possible or desirable that all of us should become botanists, and in this book the needs of the cultured humanist have been kept in mind, as well as those of the scientist. All of us are human beings first and scientists afterwards, and the laws of evolution which we have seen written in the plant world are the laws of evolution of all life — of your life and of mine. In studying these laws in their universal application you may, if you will, find some of the deepest satisfactions which life has to offer, and, as the years go by, you may slowly win to the concept of a living, organic universe whose highest values are not alien to those of human nature.

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